UNIVERSITÀ
DEGLI STUDI
DI PADOVA

**Sede Amministrativa: Università degli Studi di Padova**

Dipartimento di Psicologia Generale

SCUOLA DI DOTTORATO DI RICERCA IN: Scienze Psicologiche
INDIRIZZO: Percezione e Psicofisica
CICLO XXII

# Early predispositions for social stimuli: the case of face perception

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# Introduction

The aim of the present study is to investigate from a new perspective a long-debated issue: the specificity of the perceptual factors involved in face preferences (Morton and Johnson, 1991; Kleiner, 1990, 1993). One central issue in cognitive science is how brain does process knowledge of specific domains, as for example the visual information regarding faces. Existing evidence seems to indicate that faces are processed by anatomically and/or functionally dedicated domain-specific brain circuits, in humans (e.g., Farah, Rabinowitz, Quinn and Liu, 2000; Kanwisher, 2000) and animals[1] (adult and infant monkeys: Perrett, Hietanen, Horam and Benson, 1992; Rodman, Skelly and Gross, 1991; chimpanzees: Parr, Hecht, Barks, Preuss and Votaw, 2009; sheep: Kendrick, Da Costa, Leigh, Hinton and Pierce, 2001; see Tate, Fischer, Leigh and Kendrick, 2006 for a review).

This idea seems also to be consistent with the striking processing abilities that human beings (but also animals, see Tate, Fisher, Leigh and Kendrick, 2006 for a review; for evidence on face perception in invertebrates see Tibbetts, 2002; Van der Velden, Zheng, Patullo and Macmillian, 2008) have demonstrated in face perception (e.g. see Lewis and Edmonds, 2003 for a partial review on face detection studies in adult humans). Faces seem to automatically attract attention when naturalistic stimuli are used (Elgavi-Hershler and Hochstein, 2002; Lewis and Edmonds 2002; Langton, Law, Burton and Schweinberger, 2008[2]). In general, evidence suggests that faces can be detected and categorized very efficiently by the visual system (Purcell and Stewart, 1988; Shelley-Trembley and Mac, 1999). It seems plausible that, because of the relevance of faces for social interactions, natural selection led to the evolution of innate face-specific devices that are available prior to any postnatal experience. Nevertheless, other findings suggest that both the recruiting of specific brain areas and the high level of performance usually found in face processing could be determined not by the presence of domain

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[1] For literature on the debate about the presence of neural substrates specialized for face recognition in invertebrates see Gronenberg, Ash and Tibbetts (2007).

[2] However, it is worth noting that previous research, particularly when conducted with less naturalistic stimuli, had obtained opposite results (Brown, Huey and Findlay, 1997; Kuehn and Jolicoeur, 1994; Nothdruft, 1993).

specific mechanisms, but as an effect of the high level of expertise that human beings and social animals have about their conspecifics' faces (see Kanwisher, 2000; Logothetis, 2000; Nelson, 2001; Tovée, 1998 for reviews on this debate). The debate arosen about this expertise-theory has given more emphasis to research on the role of experience in the ontogenetic development of face processing (Gauthier and Nelson, 2001; Macchi Cassia, Turati and Simion, 2004) and on the presence of innate constrains, representations or inborn mechanisms specifically devoted to face processing prior to any experience. An important contribution in this direction may come from the study of spontaneous preferences for face-like stimuli displayed shortly after birth (as commented by Turati, 2004).

We decided to investigate this issue by employing the domestic chick (*Gallus gallus domesticus*) as an animal experimental model, due to the peculiar advantages that this species offers for the investigation of spontaneous preferences for visual stimuli shortly after hatching, controlling for the role of visual experience with faces (see below). The rationale for the use of domestic chicks is also that research on face preferences in human newborns and infants is historically rooted into studies on spontaneous preferences for hen-like objects in chicks (Johnson, 1992; Morton and Johnson, 1991; see below).

In order to investigate the specificity of the perceptual factors involved in face preferences, we thus decided to test the role of three potentially relevant perceptual properties in chicks' spontaneous preferences for face images. Our aim in doing so was to disentangle the role of three low-level perceptual properties that are considered relevant for face preferences by the human developmental literature. The properties we decided to investigate are the vertical asymmetry in the distribution of inner face features, the spatial frequencies composing stimuli and the direction of contrast polarity of face images. As regards the first two properties, it has been debated whether infants' face preferences could be a by-product of more general attentional or perceptual biases driven by such properties (Acerra, Burond and de Schonen, 2002; Kleiner, 1987; Turati, Simion, Milani and Umilità, 2002). On the contrary, sensitivity of newborns' face preference to contrast negation has been considered an index for domain specific face preferences (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). Evidence for the role of each of these properties in human infants' face preferences will be discussed in detail in the following paragraphs.

## *The debate on face preferences in human developmental literature*

### Evidence of face preferences in human newborns and infants

In the last 30 years, a number of different studies have demonstrated that, even a few hours (or minutes) after birth, when visual experience is minimal, a face-like schematic pattern moving toward the periphery of the visual field elicits greater eye-following behaviour in human newborns than do similar stimuli differing only in the non-face-like arrangement of the same internal features (that are presented in altered positions within the same outline) (Goren, Sarty and Wu, 1975; Johnson, Dziurawiec, Ellis and Morton, 1991; Morton and Johnson, 1991; Maurer and Young, 1983). Also, newborns orient their gaze more frequently and look longer toward static (schematic or realistic) face-like stimuli with their internal features arranged naturally rather than toward similar stimuli with features arranged unnaturally (Macchi Cassia, Simion and Umiltà, 2001; Macchi Cassia, Turati and Simion, 2004; Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens and Kleiner-Gathercoal, 1999; Simion, Valenza, Umiltà and Dalla Barba, 1998; Valenza, Simion, Macchi Cassia and Umiltà, 1996) or toward stimuli not resembling a face (Kleiner, 1987). Specifically, newborns presented with upright and upside-down schematic face-like configurations, matched for level of complexity, stimulus visibility, or both, show a reliable preference for stimuli displaying the upright structure of the face (Johnson and Morton, 1991; Valenza, Simion, Macchi Cassia and Umiltà, 1996). This effect has been confirmed also employing more naturalistic stimuli, such as digitally manipulated photographic images of real faces (Macchi Cassia, Turati and Simion, 2004). Moreover, some research seems to suggest that the above mentioned effects may be limited to the condition in which stimuli are presented in the periphery of the visual field (Morton and Johnson, 1991).

## The structural and the sensory hypotheses

The pattern of findings present in developmental literature on infants' face preferences has not always been of immediate interpretation: results obtained in different studies were inconsistent with regard to the stage of development during which a preference for face-like stimuli is detectable for the first time. Moreover, there seemed to be a strong effect of the experimental technique employed on results obtained (see Morton and Johnson, 1991 for a review on this topic). An interpretation of those discrepant results is described in the paragraph "The most influential instance of the structural hypothesis: the CONSPEC and CONLERN model".

According to a theory known as structural hypothesis (that will be further discussed later), the evidence available indicated that newborns detect and selectively respond to the specific structural configuration of the face, as defined by the correct relative location of the internal features representing the eyes and the mouth (consisting in darker areas arranged in a triangular-shaped configuration with one vertex pointing down). The structural hypothesis claims that the detection of faces relies on configural properties, involving the processing of features' position and spatial relations among parts.

During the past years, an alternative interpretation has been put forward to explain face preferences in newborns: the sensory hypothesis, that differs from the structural hypothesis in its assumptions regarding whether or not faces represent a special class of stimuli for newborns as compared with other visual stimuli. This hypothesis maintains that faces are not different from other visual stimuli and that they elicit preferential attention in newborns simply because their general low-level psychophysical properties, affecting the early stages of visual processing, match the sensitivity of newborns' sensory channels, increasing the visibility of faces with respect to other stimuli. One most influential version of the sensory hypothesis is based on the so called linear system model (LSM, Banks and Ginsburg, 1985; Banks and Salapatek, 1981; Gayl, Roberts and Werner, 1983; Kleiner, 1987; 1990; 1993). As the LSM and its implications are relevant for part of the research that I conducted and that will be described in this thesis, the LSM model will be further discussed in the paragraph "Introduction to Experiment 5: Role of spatial frequencies composing stimuli in face preferences".

Evidence exists in the literature in support of both the structural and the sensory hypothesis. For example, consistently with the structural hypothesis, it has been demonstrated that newborns prefer a face-like pattern even when it is compared to a stimulus of equal or higher physical salience (Valenza, Simion, Macchi Cassia and Umiltà, 1996, Experiment 3; Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens and Kleiner-Gathercoal, 1999). Morton and Johnson (1991) even claimed that part of the results obtained by supporters of the sensory hypothesis (Kleiner and Blanks, 1987) were in favour of the structural hypothesis. Kleiner and Blanks (1987) in fact, reported, among other things, that a preference was found for the configuration displaying the structure of a face when compared with another stimulus having the same level of visibility but lacking of the face structure[3]. On the other hand, the rest of the results obtained by Kleiner and Blanks (1987) were in favour of the LSM rather than of the structural hypothesis (for a detailed discussion of the results obtained by Kleiner and Blanks, 1987, see the paragraph "Introduction to Experiment 5: Role of spatial frequencies composing stimuli in face preferences"). Moreover, evidence in support of the sensory hypothesis was obtained also by Easterbrook, Kisilevsky, Hains and Muir (1999), who reported that a schematic face and other patterned stimuli containing different arrangements of the same features were equally tracked by newborns.

Nevertheless, until recent years, the overall pattern of results present in the literature, seemed to be in favour of the structural hypothesis: the LSM succeeded in explaining preferences for a certain number of visual configurations (e.g. Morison and Slater, 1985; Slater, Earle, Morison and Rose, 1985; Valenza, Simion, Macchi Cassia and Umiltà, 1996, Experiment 3; Easterbrook, Kisilevsky, Hains and Muir, 1999), but failed to entirely account for newborns' preference for face-like patterns (Kleiner, 1987; Valenza, Simion, Macchi Cassia and Umiltà, 1996). Moreover, it is also interesting to note that some data exist showing that stimuli other than faces, paired for their visibility or visual salience, are preferred by newborns on the basis of their structural

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[3] Plase note that Kleiner and Banks (1987), which are among the main theorists of the LSM, did not originally propose the interpretation of their results which is reported in this paragraph, that was later put forward by Morton and Johnson (1991) (i.e. that results obtained by Kleiner and Banks were in part in conflict with the LSM).

configurations (e.g. horizontally oriented configurations seem to be preferred with respect to vertical ones, Farroni, Valenza, Simion and Umiltà, 2000; Slater and Sykes, 1977; Slater, Earle, Morison and Rose, 1985; see also Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umilità, 2002, Experiment 1)[4].

This state of the art strongly supported the possibility that innately specified mechanisms dedicated to faces are present at birth in human babies. More specifically, newborns' spontaneous preferences for faces have been claimed to support the existence at birth of a biologically determined, experience-independent neural mechanism dedicated to face processing (Farah, 2000; Farah, Rabinowitz, Quinn and Liu, 2000; Johnson and de Haan, 2001; Johnson and Morton, 1991; Morton and Johnson, 1991; de Schonen and Mathivet, 1989)[5].

In the following paragraph we will thus deal with the structural hypothesis, by describing one of its most influential versions, that is the CONSPEC-CONLERN model proposed by John Morton and Mark Johnson in a seminal review paper published in 1991 (see also, Johnson, 2005).

## The most influential instance of the structural hypothesis: the CONSPEC and CONLERN model

According to some of the authors supporting the structural hypothesis (Johnson and Morton, 1991; Morton and Johnson, 1991; Morton, Johnson and Maurer, 1990; Johnson and de Haan, 2001) newborns' face preferences can be explained as a result of the existence at birth of a domain specific face-detecting mechanism. This mechanism would consist of a template-matching device named CONSPEC, that would contain a schematic innate

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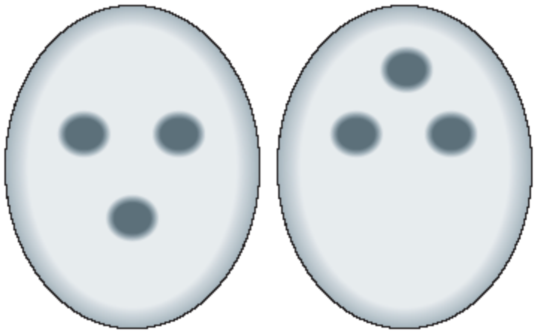
[4] In consideration of similar evidence, Kleiner and Banks (1987; Kleiner, 1990, 1993) modified the original version of the LSM by maintaining that in the case of two stimuli with identical visibility, the infant's visual preference is determined by the structure of the stimulus.

[5] For contrasting evidence see Acerra, Burnod and De Schonen (2002), which were able to simulate newborns' face preferences in a neural model just implementing some basic properties of the visual system, such as the contrast sensitivity function typical of a newborn and V1 neurons' responsiveness to spatial frequencies. The model proposed by Acerra and colleagues will be further discussed in the paragraph "Role of spatial frequencies composing stimuli in face preferences".

representation of conspecifics' appearance. In particular this representation would contain information about the structure of the faces' inner features, characterized by the presence of three high-contrast blobs in a triangular configuration corresponding to eyes and mouth, see Figure 1a).



a b

Figure 1
Schematic representation of the pair of stimuli that could be optimal for eliciting a preference for the face stimulus determined by the CONSPEC mechanism in newborns (Johnson, 2005). Stimulus a) represents a schematic face, and should be preferred by newborns' to stimulus b) that represents a face whose inner features have been turned upside down within the outline. Stimulus a) thus resembles the hypothesised schematic representation of face structure that should be encoded by CONSPEC, according to Johnson (2005).

In Johnson and Morton's (1991) view, newborns' face preference would be thus determined by the property of *facedness* (the unique structure of the face). Different stimuli have been used, through the years, in order to investigate what constitutes *facedness*. In a recent review, Johnson (2005) offers a selection of stimuli that have been used in developmental studies testing the CONSPEC-CONLERN model (see Figure 2).

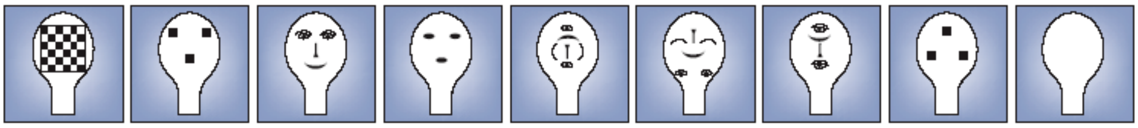


Figure 2
A selection of schematic stimuli used in developmental literature to test newborns' and infants' face preferences in relation to facedness (Johnson, 2005). Stimuli b)-d) respect the structural configuration of a face, and should thus be preferred by newborns to stimuli e)-i). Stimulus a) is a notable exception, because it is preferred to face-like stimuli due to its high physical salience (see also paragraph "Introduction to Experiment 5: Role of spatial frequencies composing stimuli in face preferences").

It has been claimed that CONSPEC would be a subcortical mechanism that receives information from the retinotectal pathway (Simion, Valenza, Umiltà and Dalla Barba, 1998; see also Johnson, 2005). This idea is mainly based on the fact that, in the developmental literature, it is believed that visual behaviour of newborn babies would be guided by subcortical structures, such as the superior colliculus (e.g. Atkinson and Braddick, 1989; Atkinson, Hood, Wattam-Bell and Braddick, 1992; Braddick, Atkinson, Hood, Harkness, Jackson and Vargha-Cadem, 1992; Bronson, 1982; Johnson, 1990, 1994, 1995). Support to the notion of the subcortical neural basis of CONSPEC is mainly given by evidence obtained in a study in which the asymmetry between the temporal and the nasal hemi visual fields of newborn babies was exploited as an index of subcortical mediation[6] (Simion, Valenza, Umiltà and Dalla Barba, 1998).

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[6] The use of the temporal-nasal asymmetry as an index of subcortical processing is motivated by the fact that such asymmetry may be an index of retino-tectal mediation (see, e.g., Rafal, Henik and Smith, 1991; Rafal, Smith, Krantz, Cohen and Brennan, 1990). The retino-tectal system seems in fact to have greater crossed input from the contralateral eye (temporal hemifield) and a smaller direct input from the ipsilateral eye (nasal hemifield) with respect to the geniculostriate system. However see Williams, Azzopardi and Cowey (1995) for contrasting evidence. Williams and colleagues conducted anatomical studies on macaque monkeys, and the results they obtained may put in doubt the notion that temporal-nasal asymmetry reflects retino-tectal mediation. Nevertheless, this does not exclude the possibility that even if the temporal-nasal asymmetry may not be a marker for the retino-tectal pathway, it may still be a marker for some other extrageniculate visual pathway.

Simion and her colleagues demonstrated that a preference for looking at a schematic face-like stimulus over a similar but non-face-like scrambled stimulus, was observed only if the stimuli were presented in the temporal visual fields of newborn babies, and not in their nasal visual fields. In a recent review Johnson (2005) provided evidence in favour of the hypothesis that a "quick-and-dirty"[7] subcortical route would be involved not only in face preferences displayed by newborn babies, but also in face detection in adult human beings. The sub-cortical route hypothesized by Johnson (2005) would involve the superior colliculus, pulvinar and amygdala. This route would rapidly process low-spatial-frequency information, allowing for a quick detection of the presence of a face in the periphery of the visual field (the face could be subsequently foveated for closer inspection). The activity of this subcortical route would modulate the activation of cortical areas specialized for face processing in adults and would drive the development of the very same areas during infancy, also by means of providing an extensive experience with face stimuli to the developing cortex (Johnson, 2005).

It has thus been claimed that CONSPEC's main aim would be that of orienting newborns' gaze toward face-like patterns appearing in the periphery of the visual field (in line with its putative neural basis in the superior colliculus). As a consequence, it could orient, but not hold, newborns' attention on faces. In line with this hypothesis Macchi Cassia, Simion, and Umiltà (2001) proved that the results, previously obtained by Valenza, Simion, Macchi Cassia and Umiltà (1996), indicating a longer fixation time for faces (and thus in contrast with the orienting mechanism hypothesis), were indeed due to the action of an orienting mechanism[8]. During the first months of life the subocrtical CONSPEC would

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[7] By "quick-and-dirty" route it is here meant a brain route characterized by a very fast, but not very accurate, processing.

[8] In this study Macchi Cassia, Simion and Umilità (2001) used a revised version of the preferential looking technique usually employed in experiments investigating newborns' looking preferences for faces. In the revised version of this task the same stimulus (i.e. in this case a face-like or a non-face-like pattern) is simultaneously presented at the two sides of a screen. Using this technique, the authors were able to demonstrate that the longer fixation times displayed by newborns toward the face-like stimulus actually derived from the sum of a greater number of brief fixations rather than from the sum of a small number of long fixations.

thus act as a guide by orienting attention toward stimuli that match faces' structure. In that way it would bias the visual input to the developing cortex, which would benefit from repeated exposure to faces, favouring the emergence of cortical circuitry specialized for face processing.

Morton and Johnson (1991) also theorized the presence of another independent mechanism, named COLNERN, that would be in charge of learning the features of those objects toward which CONSPEC has oriented the infant's attention.

The presence of this second mechanism (CONLERN) and its interaction with CONSPEC explained also the discrepant results described in the literature regarding the stage of development during which a preference for face-like stimuli is detectable for the first time and its inconsistent time course through the first months of life (especially when different experimental procedures are employed). According to some evidence, in fact, a preference for looking at face-like stimuli would be absent at 1 month of age and would appear at 2 months of age (e.g. Maurer and Barrera, 1981) or even later (e.g. Haaf, 1974; 1977; Haaf, Smith and Smitty, 1983). However, other studies demonstrated a preferential tracking of face stimuli in few-hours-old babies (Goren, Sarty and Wu, 1975). A preference for faces would thus be evident at birth and after two months, but not at one month of age.

According to the interpretation proposed by Morton and Johnson (1991) of the incongruent results described above, the different experimental techniques employed by the various experimenters were selectively sensitive to the action of one of the two above mentioned mechanisms (i.e. CONSPEC and CONLERN) (for a review see Morton and Johnson, 1991).

In particular, CONSPEC, due to its subcortical neural basis in the superior colliculus, would be effective in orienting attention toward faces presented in the peripheral visual field. Tasks appropriate for activating CONSPEC would thus be tracking tasks, in which the stimuli are moved toward the periphery of the visual field (in this case babies have to move their eyes in order to follow the stimuli, and the extent of this eye-following response is measured). Using this kind of task, Morton and Johnson (1991) were able to demonstrate face preferences in newborn babies, replicating the finding of Goren, Sarty and Wu

(1975). Using a very similar task, in which stimuli are kept static and the infant is rotated, Morton and Johnson (1991; original data reported in Johnson, Dziurawiec, Ellis and Morton, 1991) were also able to obtain a preferential orienting for faces in 4-5 week old infants (i.e. infants of about 1 month of age). On the basis of this result, Morton and Johnson (1991) suggest that CONSPEC would be responsible for the preference observed in babies from birth up to one month of age (i.e. 4-5 weeks). CONSPEC would be, in fact, active from the very moment of birth, but its influence would be detectable only when presenting the experimental stimuli in the peripheral visual field[9] (or moving toward the peripheral visual field).

Consistent with this explanation, by using static stimuli presented in the central visual field, Morton and Johnson (1991) did not obtain any evidence of a preference for face-like configurations in one-month-old babies, consistently with previous results by Maurer and Barrera (1981). However, this same testing technique (i.e. a central presentation of static stimuli) was sufficient to reveal a preference for faces in 10-week old babies (i.e. babies of about two months of age).

On the other hand, the tracking task described above (that was effective in eliciting a preference for faces in babies up to 5 weeks of age) was not effective in older babies (of 6, 10 or 18 weeks of age) (Johnson, Dziurawiec, Ellis and Morton, 1991; Morton and Johnson, 1991).

Thus the technique that is effective form birth to 6 weeks of age (i.e. presenting stimuli in the peripheral visual field by a tracking task), ceases to be effective after this age. However, as babies reach the second month of life, another technique (i.e. presenting static stimuli in the central visual field) becomes effective.

According to Morton and Johnson (1991), this second technique would be effective in older babies because it would activate the CONLERN mechanism. In fact, Morton and Johnson (1991) state that CONLERN would start to be active at about 2 months of age (due to the maturation of the cortical structures that constitute its neural basis). Moreover, the development of cortical

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[9] According to Morton and Johnson (1991) the crucial factor would not be the fact that stimuli move through the visual field, but that they end up in the periphery of the visual field. In fact the same results could be obtained using static stimuli presented in a sufficiently peripheral position (e.g. Kleiner, 1987).

structures that constitute the neural basis of CONLERN, would inhibit (or compete with, Johnson, Farroni, Brockbank and Simion, 2000) the subcortical structures that are supposed to be the neural basis of CONSPEC, determining a decline in CONSPEC's influence after 2 months of age. This is why the tracking tasks that were effective in eliciting newborns' preference, stop to be sufficient to elicit a preference in older babies.

The CONSPEC-CONLERN model (Johnson and Morton, 1991), even if not beyond criticisms, has thus been able to account for a great part of the developmental literature on face preferences in newborns and infants. For this reason such a model has been the starting point of most of the research conducted in the following years on this topic. As regards criticisms to this model, a main source of debates in the developmental literature has been the role of some general non-face-specific properties of stimuli in determining face preferences. The role of some of those properties in driving domestic chicks' face preferences will be one of the central issues investigated in my thesis. For a detailed description of debates on this regard, see paragraphs "Role of vertical asymmetry of inner facial elements in face preferences", and "Role of spatial frequencies composing stimuli in face preferences".

## Broader theoretical approaches underlying the debate on face preferences in human developmental literature

The CONSPEC and CONLERN model is based on a neuroconstructivist approach to infants' development, according to which domain-specific mental structures gradually emerge from the interaction between innately specified constraints and the input provided by the species-typical environment. This position has the advantage to imply that human beings evolved an innate device specifically selective for faces, but to maintain at the same time the idea that visual experience plays a prominent role in development of face processing. Thus, this approach excludes the existence of a face-specific cortical system that is active from birth[10]. Particularly, in a recent review by

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[10] The opposite view is represented by a work of Farah, Rabinowitz, Quinn and Liu (2000). This author, on the basis of a single case study demonstrating a lack of plasticity in the development of face

Johnson (2005) some evidence has been described pointing to the existence of a rapid subcortical route for face processing in adults that modulates cortical processing. In the same paper it has also been suggested that newborns' preferences might rely on a precursor of the subcortical route described in adults. This route might be important for establishing the network of cortical regions that constitute the adult social brain (in fact disturbances to this pathway might contribute to some types of atypical development).

However, this perspective has been criticised because it assumes that a highly specific starting point is necessary to initiate development in the domain of face processing (Macchi Cassia, Turati and Simion, 2004). In fact, according to the neuroconstructivistic approach assumed by Johnson, the development of the face processing system requires an initial input that is already domain-specific in nature (a specific representational bias at a lower neural level, such as for example the innate representation of faces' structure encoded by CONSPEC).

As opposed to this view, an alternative approach has been proposed, always within a experience-expectant neuroconstructivistic conceptual framework: according to this perspective (Nelson, 2001; 2003), the neural and perceptual specialization for face processing observed in adults arises during development from a non-specific system that becomes progressively tuned to upright human faces, due to the extensive experience with this kind of stimuli available to human infants (within a critical time window) in the species-typical environment[11]. Within this approach, it was suggested that exposure to faces during development, interacting with the partial functioning of neural pathways, produces a perceptual narrowing for this class of stimuli. As a consequence there would be an increase in the selectivity of infants' neural responses[12] (e.g. de Haan, Pascalis and Johnson, 2002; Halit, Csibra, Volein and Johnson, 2004) and behavioural responses (Pascalis, de Haan and Nelson, 2002). This increase in selectivity would be expressed as a functional shift from responding to a broad range of visual information to responding only to the specific kind of

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recognition abilities, claimed that the anatomical (cortical) localization of brain circuits specialized for face recognition is explicitly specified in the human genome.

[11] Another crucial factor would be of course the potentiality of cortical tissue to become specialized for face processing.

[12] Similarly, the cortical circuits that in infants would process face stimuli should also become more anatomically localized as a consequence of the perceptual narrowing process.

information conveyed by upright human faces. This produces, in turn, a more precisely defined face category, based on the kind of faces that the developing infant has been more exposed to in its environment. Only this kind of faces will benefit of more efficient processing strategies. This alternative view differs from the original model of face-processing development proposed by Johnson and Morton (1991; Johnson and de Haan, 2001), because it would assume that a general initial input (e.g. domain-general predispositions), rather than a specific initial input (e.g. a specific subcortical bias toward faces), is sufficient to the development of the domain-specific face recognition system (Macchi Cassia, Kuefner, Westerlund and Nelson, 2006a). In line with this reasoning it has been suggested that the presence at birth of non-specific constraints on visual processing (determined by the general functioning of the visual system) might be sufficient to produce the emergence of the functional specialization for faces observed later in development, tuning the system toward certain aspects of the external environment and allowing the extensive experience necessary to the development of specialized processes. Some models based on this perspective (e.g. Turati, Simion, Milani and Umiltà, 2002) are relevant to part of the work that I will describe in my thesis, and will be thus discussed in detail in the paragraph "Introduction to Experiments 1-4: Role of vertical asymmetry of inner facial elements in face preferences".

Evidence in favour of this perceptual-narrowing account comes from different sources, including behavioural and ERP studies investigating the developmental course of the so called "other-species effect" (consisting in a lower level of performance for processing faces of another primate species with respect to the processing of conspecifics' faces). Those studies demonstrate that behavioural (Pascalis, de Haan and Nelson, 2002) and cortical (de Haan, Johnson and Halit, 2003; de Haan, Pascalis and Johnson, 2002; Halit, de Haan and Johnson, 2003) specialization for the processing of upright human faces (as opposed to that of non-human primate faces) is present in adults, but seems to emerge only gradually during the first year of life. This perspective appears to be appealing to some authors (Nelson, 2001; Turati, 2004) also because it is consistent with models that explain the development of another domain-specific cognitive competence, namely language, on the basis of general experience-expectant sensory and learning mechanisms (Werker and Vouloumanos, 2001)[13].

It has to be noticed that the two approaches described in this paragraph (the approach proposed by Johnson and the perceptual narrowing approach), while differing at the level of the precise mechanisms hypothesised, do share nevertheless some fundamental assumptions (e.g. the assumption about the progressive increase in specialization and localization of cortical circuits deputed to face processing) and should not be considered as completely opposite views.

### *Investigations on face perception in animal species*

Some animals seem to have quite remarkable face processing abilities. For example, see the review on behavioural and neurophysiological evidence of face identity and face emotion processing in animal species, published by Tate, Fischer, Leigh and Kendrick (2006) (see also Tibbetts, 2002; Van der Velden, Zheng, Patullo and Macmillian, 2008 for evidence on individual face recognition in two invertebrate species, the wasp *Polistes fuscatus* and the crayfish *Cherax destructor*, respectively). According to Tate, Fischer, Leigh and Kendrick (2006), behavioural and neuropsychological studies on animal models such as monkeys and some ungulate species (sheep and goats)[14],

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[13] It has been also claimed that some behavioural findings regarding the disappearance of the preference for highly schematic faces by the 6th week of age (Johnson, Dziurawiec, Ellis and Morton, 1991; Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens and Kleiner-Gathercoal, 1999) or the absence of sensitivity for contrast polarity before the 12th month of age (Dannemiller and Stephens, 1988; Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens and Kleiner-Gathercoal, 1999) could be further elements in support of the perceptual-narrowing approach. This would suggest that during the first year of development, infants' behavioural responses start to depend more on the extent to which various characteristics of the stimuli resemble those included in real faces. However, it should be remembered that a different explanation is already available for the first phenomenon (see Morton and Johnson, 1991), whereas more recent studies demonstrated a sensitivity to contrast polarity in face stimuli already in newborns (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). For further discussion of evidence of the presence of sensitivity to contrast polarity information in newborns see the paragraph "Introduction to Experiments 6-11: Role of contrast polarity in face preferences".

[14] Recently, evidence has been published proving face processing abilities (individual recognition and species recognition based on the appearance of the face) also in the domestic cattle (*Bos taurus*) (Coulon, Deputte, Heyman and Baudoin, 2009; Coulon, Deputte, Heyman, Delatouche, Richard and

show that specialized skills and neural systems for processing information conveyed by faces (identity, species, sexual and emotional states) have evolved in animal species other than human beings. Moreover, similarities exist in the ways faces are processed by the brain in human and non-human animals (Tate, Fischer, Leigh and Kendrick, 2006).

In particular, as regard face preferences, existing evidence indicates that, to some extent, various animal species such as sheep (Kendrick, Atkins, Hinton, Broad, Fabre-Nys and Keverne, 1995; Porter and Bouissou, 1999; Da Costa, Leigh, Man and Kendrick, 2004), apes and monkeys (e.g. see Lutz, Lockard, Gunderson and Grant, 1998; Bard, Platzman, Lester and Suomi, 1992) may show spontaneous preferences for social stimuli, such as face-like stimuli.

Investigations of face perception in sheep and lambs have been rather extensive, suggesting that social recognition in these species relies on the appearance of the face region, at least to some extent. Consequently, sheep present quite remarkable face recognition abilities, being able to discriminate between faces of different species, sheep breeds, gender and individuals (e.g. Kendrick, Atkins, Hinton, Broad, Fabre-Nys and Keverne, 1995; Kendrick, Leigh and Peirce, 2001). The eyes are the most important single feature used in recognition by this species (Kendrick, Atkins, Hinton, Broad, Fabre-Nys and Keverne, 1995; see Tate, Fischer, Leigh and Kendrick 2006 for a review). Sheep also show indexes of configural face processing (e.g. they show an inversion effect for face stimuli[15]) and of right hemisphere advantage in face perception tasks (Kendrick, Atkins, Hinton, Heavens and Keverne, 1996; Peirce, Leigh and Kendrick, 2000). The inversion effect shown by sheep (but not the right hemisphere advantage) extends also to human faces (Kendrick, Atkins, Hinton, Heavens and Keverne, 1996; Peirce, Leigh, da Costa, and

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Baudoin, 2007) and in dogs (Racca, Amadei, Ligout, Guo, Meints and Millis, 2010). Dogs showed individual recognition of both human and dog faces. Dogs' specialized skills for the analysis of human faces may be also the cause of the left-gaze bias that dogs show when inspecting human (but not dog) faces (Guo, Meints, Hall and Mills, 2009).

[15] The face inversion effect is a reduced performance in the identification of faces when these are presented upside-down (i.e. rotated of 180° on the vertical axis) with respect to when these are presented upright (Yin, 1969). In humans, this effect is much more marked for faces than for other object categories, and is considered a hallmark of the domain-specific processes applied to faces. The face inversion effect is also considered an index of configural face processing (Rossion and Gauthier, 2002).

Kendrick, 2001) [16]. In lambs, the ability to recognize individual faces would emerge during the first months of life (Kendrick, 1998). The work conducted on ungulate species is particularly relevant because it disconfirms the theory according to which specialized processing of visual cues originated from faces of other conspecifics would be an uniquely primate feature (see Tate, Fischer, Leigh and Kendrick, 2006 for a discussion).

Except for studies on sheep, most of the works available in the animal face-perception literature are on primate species. For example non-human primates seem to have face recognition abilities (e.g. Phelps and Roberts, 1994; Weiss, Kralik, Garibaldi and Hauser, 2001). However, contrasting results are reported in the literature as regards the presence of a face inversion effect (a hallmark of configural face processing) in non-human primates (Perrett, Mistlin, Chitty, smith, Potter, Broennimann, and Harries, 1988; Rosenfeld and Van Hoesen, 1979; Bruce, 1982) A complete review of all the evidence regarding various aspects of face processing in primates would be out of the aims of the present work. However, some studies are particularly relevant because they investigate spontaneous preferences for faces and/or they used infants (or visually naïve) subjects. Those studies are discussed in the following paragraphs.

Faces seem to be a relevant stimulus for infants of primate species relatively early during development, in line with what is known for human babies. Socially deprived infant monkeys (visually naïve with respect to the appearance of conspecifics, but with 5-9 days of visual experience about the appearance of human beings) have been shown to respond at an early age to images of conspecifics (Sackett, 1966). Infant chimpanzees start to recognize their mother's face between 4-8 weeks of age (Myowa-Yamakoshy, Yamaguchi, Tomonaga, Tanka and Matsuzawa, 2005). In line with this result, neurons responsive to faces can be found in the brain of monkeys as young as 6 weeks of age (Rodman, O'Scalaidhe and Gross, 1993).

Some studies also demonstrated the presence of a preference for faces in juvenile or infant primates. Adolescent rhesus monkeys tend to look more at normal faces than at scrambled ones (Keating and Keating, 1982). Similarly,

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[16] Recent evidence showed that also another domesticated species, i.e. the domestic dog, presents an inversion effect for both human and conspecific faces. However, this inversion effect was not specific for faces, extending also to other objects (Racca, Amadei, Ligout, Guo, Meints and Millis, 2010).

Bard, Platzman, Lester and Suomi (1992) found that newborn chimpanzees prefer social stimuli, such as faces with respect to non-social stimuli, such as a red ball. Lutz, Lockard, Gunderson and Grant, 1998 demonstrated that 2-10 week old macaques prefer to fixate normal drawings of conspecific faces with respect to distorted drawings. Myowa-Yamakoshi and Tomonaga (2001a) demonstrated that a two-week-old gibbon (who had non-controlled visual experience with faces) showed a preference for schematic or photographic images of faces with respect to stimuli that differed only in the arrangement of inner facial features (similar to the stimuli used with newborn babies, see Morton and Johnson, 1991) (Figure 3). However, as regards stimuli obtained from photographic images, the preference for an intact face over a scrambled one was evident only when using images of a familiar face (i.e. the face of the human caregiver), but not when stimuli were obtained from faces of unfamiliar individuals. This was true for both unfamiliar human or unfamiliar gibbon faces.

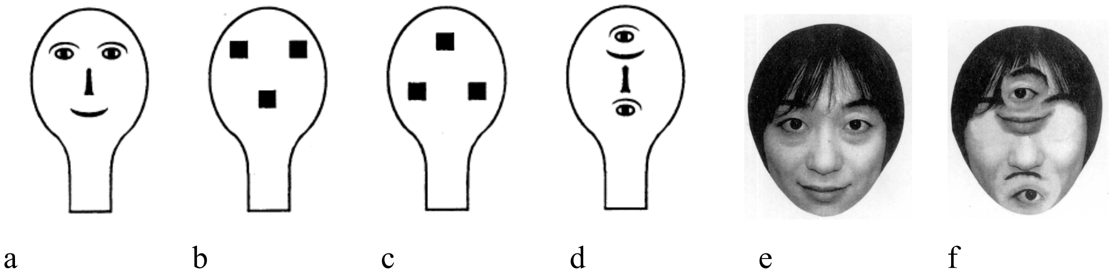

Figure 3
Reproduction of the stimuli employed by Myowa-Yamakoshi and Tomonaga (2001a). Stimuli a) and b) represent schematic faces, whereas stimuli c) and d) are, respectively, upside-down and scrambled versions of the same stimuli. Stimuli e) and f) represent, respectively, the photographic image of the face of a human being familiar to the subject (i.e. the face of the human caregiver) and the scrambled version of the same stimulus.

It is worth noting that results obtained by Myowa-Yamakoshi and Tomonaga, (2001a) are very similar to those obtained in human infants (Morton and Johnson, 1991). The same authors (Myowa-Yamakoshi and Tomonaga, 2001b) also demonstrated that an infant gibbon preferred a stimulus displaying a face possessing two eyes with respect to an image with no-eyes (i.e., possessing only a mouth and a nose), in line with the central role of the eyes in face preferences. Another interesting work, run on infant macaques by Kuwahata, Adachi, Fugita, Tomonaga and Matsuzawa (2004), investigated looking preferences for schematic faces with respect to scrambled stimuli. For a reproduction of stimuli employed by Kuwahata, Adachi, Fugita, Tomonaga and Matsuzawa (2004), see Figure 4. This work also assessed the role of face configuration and face features in this kind of preference. The authors proved that monkeys younger that one month of age prefer face-like configurations in which internal features (eyes and mouth) are schematically represented by three black squares, with respect to a control stimulus in which the three black blobs are aligned on the vertical axis (thus not possibly representing a face). On the contrary, after one month of age, monkeys' preference is evident only with more detailed stimuli, such as simple drawings of faces. It is interesting to note that a similar developmental pattern was observed also in human newborns: stimuli of increased complexity were required to elicit face preferences in infants older than 5 months (see Morton and Johnson, 1991). One additional element of interest in this study is the fact that, even if the authors did not assess directly this issue, the stimuli employed can be classified also in terms of the vertical asymmetry in the distribution of inner elements (the number of elements in the upper versus the lower part of the stimulus, is considered a relevant factor in human newborns' face preferences, Turati, Simion, Milani and Umiltà, 2002[17]). In fact, in one of the two stimuli pairs employed (Pair b, Figure 4 b1-b2), a face like configuration was preferred to another top-heavy configuration (i.e. another stimulus presenting an higher number of elements in its upper part).

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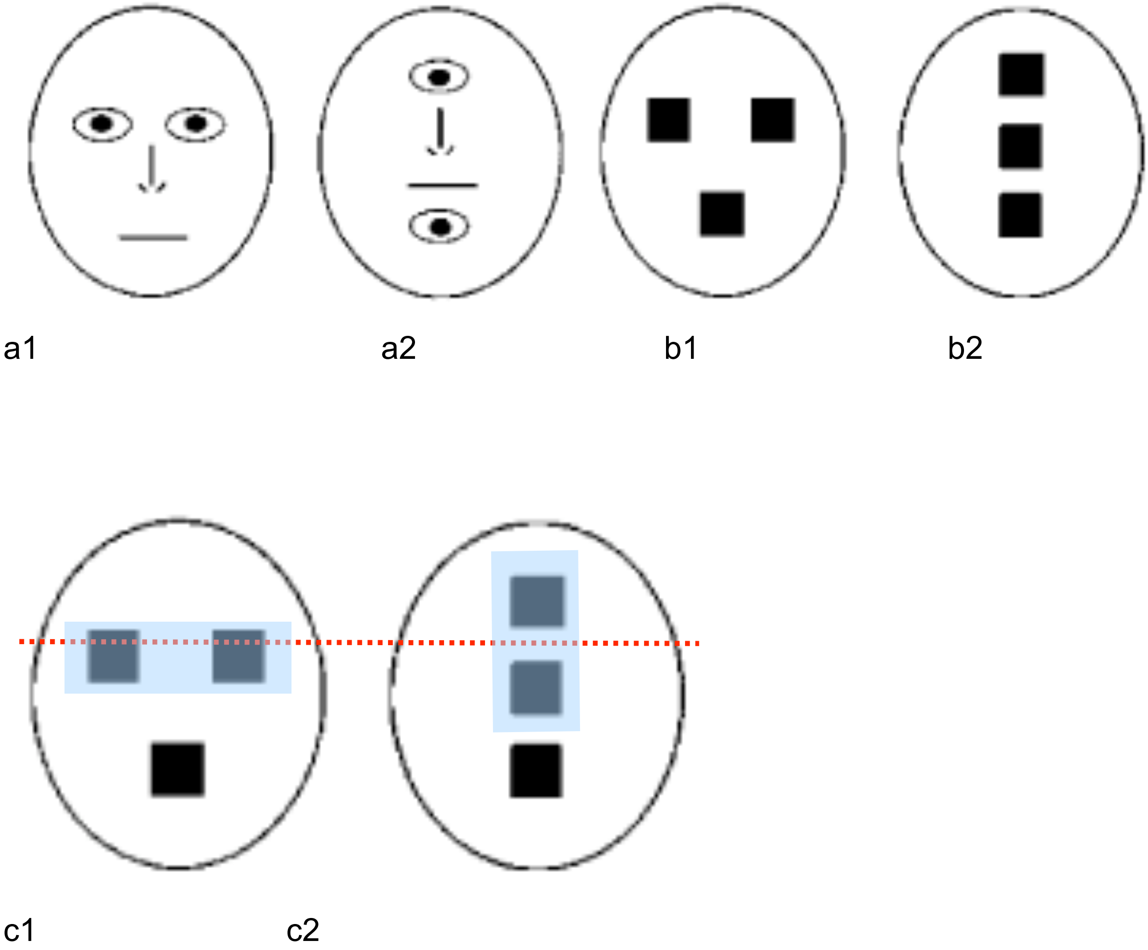
[17] The role of the number of elements present in the upper and lower half of images is relevant to the work conducted for my PhD project, and will be thus further discussed in the paragraph "Role of vertical asymmetry of inner elements in face preferences".



a1 a2 b1 b2

c1 c2

Figure 4

Reproduction of the two pairs of stimuli (pair a and b) employed by Kuwahata, Adachi, Fugita, Tomonaga and Matsuzawa (2004). Each pair of stimuli consists in a face-like schematic stimulus (a1, b1) and a non-face-like control stimulus (a2, b2) that contains the same inner elements arranged unnaturally (in scrambled positions). Stimuli in pair b are of particular interest because both configurations are top-heavy (that is to say that both present more inner elements in their upper part). In fact, the mean height of the two upper blobs representing inner features (highlighted in blue in stimuli c1 and c2) is even higher for the non-face-like configuration with respect to the face-like one (as shown by the dotted red line in stimuli c1 and c2). Stimuli c1 and c2 are again reproductions of pair b stimuli. For illustrative pourposes I have superimposed on stimuli c1 and c2 some graphic elements (i.e. a red dotted line and two blue shaded areas) in order to make it easier to understand the description of pair b stimuli.

Unfortunately, in the study by Kuwahata, Adachi, Fugita, Tomonaga and Matsuzawa (2004), animals were allowed to have full visual experience of conspecifics' (and probably also of human experimenters') faces prior to the moment of the test, thus making the role of previous visual experience in the results obtained very difficult to assess.

Finally, a recent work by Sugita (2008) produced striking evidence in favour of experience-independent face processing abilities in infant monkeys (*Macaca fuscata*). Moreover, the work by Sugita (2008) produced also evidence in favour of the presence of face preferences in visually naïve monkeys and of the crucial role of the subsequent interaction between these innate abilities and the perceptual experience that monkeys had over a sensitive period. Both human and monkey faces resulted to be spontaneously preferred over other kinds of visual objects (like pictures of non-animate objects), without the animals having visual experience with faces prior to the moment of the test.

This result seems to be strongly in favour of the presence, in monkeys, of a CONSPEC-like unlearned mechanism that directs attention toward face-like stimuli, in line the hypothesis proposed by Morton and Johnson (1991). Moreover, the preference for face-like objects displayed by monkeys tested by Sugita (2008) appeared to be non-species-specific. In fact, both human and monkey faces were equally preferred by visually naïve monkeys. This is in line with the hypothesis that a very broad representation of faces' structure (like that encoded by CONSPEC according to Morton and Johnson, 1991, see Figure 1) would be at the basis of face preferences. However, part of the data obtained by Sugita (2008) supported the perceptual-narrowing hypothesis (see paragraph "Broader theoretical approaches underlying the debate on face preferences in human developmental literature", and see also Nelson, 2001). In fact, monkeys that were selectively exposed to faces of only one species (i.e. either human or monkey faces), developed a preference for the kind of faces to which they had been exposed. This is in line with some evidence obtained in cross-fostering studies in sheep and goats that preferred faces of the species providing maternal care. Moreover, after this selective exposure, the monkeys tested by Sugita lost the ability to process faces of the species to which they had not been exposed (Kendrick, Hinton, Atkins, Haupt and Skinner, 1998; Kendrick, Haupt, Hinton, Broad and Skinner, 2001).

These results are surely impressive. Some methodological issues, though, in the procedure employed by Sugita (2008) could prevent the author from claiming that the kind of preference observed was completely innate. For example, monkeys were allowed to spend some hours in the presence of their mother before the beginning of the visual deprivation period. Moreover, the author himself rises a concern about the possibility that the young monkeys could have gained some sort of information about the structure of faces by manual tactile exploration of their own face or from proprioceptive information originated by their very well developed facial expressive muscles. It is thus worth noting that, if on one hand the relatively short phylogenetic distance between humans and monkeys (compared with other animals) makes them an interesting model for comparative studies on this kind of topic, on the other hand monkeys could not always be the most profitable model for the investigation of the innateness of hypothesized mechanisms.

Finally, it should be noticed that none of the studies here reported conducted on non-avian animal species has sufficiently controlled for the role of low-level perceptual properties (such as those investigated in human newborn literature and in my thesis) in determining preferences for faces (this is particularly true for studies that compared preferences for faces with respect to other non-face objects, e.g. Sugita, 2008).

## Face perception in avian species

Surprisingly, little research has been devoted to the investigation of face perception in avian species, with few notable exceptions that will be now described. It has to be noticed that, even though a certain number of studies have been conducted in which pigeons were trained to respond to human faces, the aim of these studies was mainly to investigate categorization abilities in pigeons (e.g. Jitsumori and Yoshihara, 1997 for pigeons' categorization of facial expressions; Huber, Troje, Loidolt, Aust and Grass, 2000; Loidolt, Aust, Meran and Huber, 2003; Troje, Huber, Loidolt, Aust and Fieder, 1999 for categorization of faces on the base of gender: in this case pigeons seem to rely more on textural than on shape cues for categorization; the features used by pigeons for categorization of faces based on gender or expression seem also to overlap with those used by humans, Gibson, Wasserman, Gosselin and

Schyns, 2005). Another topic investigated by this kind of studies was pigeons' recognition of individual human faces on the basis of different features (e.g. pigeons seem unable to form a three dimensional representation of faces, Jitsumory and Makino, 2004; Loidolt, Aust, Steurer, Troje and Huber, 2006). Such studies can usually tell us very little about spontaneous face perception or face preferences in pigeons and thus they will not be extensively reviewed here.

In analogy to what observed for human beings, faces could be a socially relevant stimulus for avian species. In fact, evidence is there in the literature demonstrating that in some avian species individual recognition is based on features present in the face region (see below). Besides individual recognition, other biologically relevant signals may be conveyed by the face region of conspecifics in avian species (Brown and Dooling, 1992; 1993). For example, in territorial birds, such as the Glaucous-winged gull (*Larus glaucescens*), the head region of the "invader bird" seems to be the crucial stimulus for eliciting the aggressive behaviour that individuals of this species display toward conspecifics invading their territory (Stout and Brass, 1969).

In 1953, Guhl and Ortmann demonstrated that domestic pullets (*Gallus gallus domesticus*) use features of the neck and head of conspecifics to recognize familiar individuals. In fact, alterations in the head and neck regions (and particularly on the comb) resulted to be more effective in abolishing recognition of the subject by other flock members than those performed on the trunk or tail. In line with this evidence is the fact that hens were found to examine the head region of other hens, when they encountered them in an unfamiliar environment, probably in order to perform individual recognition (Dawkins, 1995). This tendency to use features present in the head region as a cue for individual recognition could be due to the fact that hens establish their position in the dominance-hierarchy of the flock (the pecking order) by a form of fighting in pairs, which involves aggressive pecking at the head of another individual (Rushen, 1982). Thus, when learning the identity and dominance position of another bird, hens would store information on the appearance of its head region, and they would then rely on such information for future recognition of this same individual.

Moreover, roosters of the same species (*Gallus gallus domesticus*) can learn to use configurations of facial features in order to discriminate between photographic images representing conspecific heads in a simultaneous discrimination task for food reinforcement (Candland, 1969). Unfortunately, only profile images were employed in this study and only the role of features such as comb, beak and wattle was investigated, limiting the level of inference that can be drawn form the results of this study. In a more recent study, Bradshaw and Dawkins (1993) tested hens' performance in a discrimination task of slides representing images of the head region of different conspecifics. However, in this study, after the initial learning hens did not show generalization to stimuli representing novel views of the same individuals that were used as training stimuli. Thus, the authors of this study concluded that the hens were not able to recognize the photographic images used as stimuli as representations of their group members (Bradshaw and Dawkins, 1993). A subsequent study confirmed the possibility, for hens, to be trained to recognize individual conspecifics on the basis of the appearance of the head and neck region (Dawkins, 1996). Both frontal and profile views seemed to be sufficient for individual recognition. However, hens succeeded in the recognition task only when heads of live birds were used as stimuli, but not when photographic images were used as stimuli (in contrast to what reported by Candland, 1969)[18].

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[18] Also a previous study had demosntarted that chickens can be trained, for food reinforcement, to discriminate slides representing images of different individual conspecifics (Ryan and Lea, 1994). In this study however, slides used as stimuli represented the whole body of the stimuli-birds, not only the head region (as a consequence it was not possible to determine the role of the head region in the discrimination performance). After learning, transfer was observed for stimuli representing novel views of the same individual conspecifics that were used as training stimuli. The same study proved also that chickens can be trained to discriminate slides representing images of different pigeons, but chickens' performance was poorer for pigeons' than for chickens' faces, showing thus an advantage for the individual recognition of conspecifics. It is finally worth noting that chickens' performance in this task was always higher than pigeons' performance, even when photos of pigeons were used as stimuli. This suggests that visual recognition of individuals may be a particularly well developed ability for domestic chickens. It has been hypothesised that this could be due to the fact that chickens are a precocial species, whereas pigeons are an atricial species: precocial animals must learn very rapidly, early in life, to recognize individual conspecifics, such as parents (Ryan and Lea, 1994).

Summarizing, it seems that face features or a configuration of face features can be used (Candland, 1969; Dawkins, 1996), and tend to be used (Guhl and Ortmann, 1953; Dawkins, 1995) by domestic chickens in order to recognize different individuals and to guide social interactions, in line to what observed for our own species.

Similarly, it has been demonstrated that budgerigars (*Melopsittacus undulates*, a small species of parrot) are able to distinguish between photographic or schematic images of conspecifics on the basis of face features (Brown and Dooling, 1992; 1993). Colour of the face (that could be more salient than colour of the body), markings pattern of plumage, colour of the iris and size of the pupil resulted influential factors in birds' ability to discriminate among conspecific faces (note that when manipulated simultaneously the informative values of different features changed). It is relevant to note that all these features offer potential biologically relevant information to this species (e.g. the colour of the iris indicates age and pupil constriction is a signal used in courtship rituals). Moreover, for budgerigars differences between conspecific faces were more salient than differences between zebra finches' faces and conspecific faces were perceptually distinct from the faces of other avian species. Of particular interest is the fact that an inversion effect was observed: discrimination performance decreased when faces were presented in an upside-down orientation (180° rotated). Similarly, scrambled faces were more difficult to discriminate than normal faces. This evidence is remarkable because it points toward the presence of configural face-processing in avian species (configural processing is one of the traits that are considered to be markers of the domain-specific nature of face processing in humans). The effect of social experience on configural processing was also investigated: isolation reared birds failed to show decrease in discrimination performance with scrambled faces. Two possible interpretations emerge for this result: experience could be a crucial factor for the processing of facial configuration, or isolation reared birds could be not comparable to normal birds in their social skills in general.

In contrast to what observed in budgerigars (Brown and Dooling, 1992; 1993) it is interesting to note that Phelps and Roberts (1994) reported the absence of face inversion effect in pigeons *(Columba livia*) (whereas they confirmed the presence of this effect in a monkey species). On the basis of this result, the authors suggest that different face processing mechanisms are present in primates with respect to avian species: in fact, the face inversion effect would be, according to their theory, derived from the action of a specialized face processing mechanism absent in avian species. This hypothesis is also supported by the results of a control experiment (reported in the paper by Phelps and Roberts, 1994 as “unpublished data”), which shows the absence of the face inversion effect in pigeons even when tested with bird faces. However, the authors did not specify whether the face stimuli used in this control experiment were pigeon faces or faces of other avian species. Moreover, the interpretation proposed by Phelps and Roberts (1994) about the uniquely primate nature of the face inversion effect does not fit with the data reported by Brown and Dooling (1992; 1993) about the presence of the face inversion effect in budgerigars.

It is interesting to report that recently a study on the same species used by Phelps and Roberts (1994) (i.e. pigeons) showed that, when pigeons are trained for food reinforcement to peck only photographic images of scenes containing humans, adult pigeons spontaneously tend to peck on the area of the image where the faces of the human beings are presented (Dittrich, Rose, Bushmann, Bourdonnais and Güntürkün, 2010). In this study, removal of the face impaired performance more than removal of other parts of the human figure. This result may imply the presence of a spontaneous preferential attention for faces in pigeons. However, further work is needed to clarify this issue, mainly because the investigation of spontaneous attentional biases was not the main aim of the study, and thus prior experience of animal subjects was not sufficiently controlled.

As regards conspecifics’ recognition, it has been demonstrated that pigeons can be trained, for food reinforcement, to discriminate between colour slides of pigeons’ faces (Watanabe and Ito, 1991)[19]. In this study the discrimination task

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[19] However, for contrasting evidence on pigeons’ difficulty to discriminate slides representing individual conspecifics, see Ryan and Lea (1994). In this study, only one pigeon out of six succeeded in discriminating slides representing different pigeons, whereas, surprisingly, pigeons’ performance was better for slides representing images of chickens. The results of this study are difficult to interpret, also because pigeons were able to readily discriminate two live pigeons, but not stuffed pigeons. No single

was easier for pigeons when stimuli that are easily discriminated by human observers were used, whereas the task was more difficult for pigeons when stimuli were images that human observers find difficult to recognize (thus pigeons and humans may apply similar strategies for the recognition of pigeons' faces). Moreover, when scrambled pictures were used as stimuli, pigeons did not respond. According to the authors, this result suggests that pigeons saw the colour slides of conspecific faces (but not the scrambled stimuli) as representatives of real birds. The impairment observed for scrambled stimuli may also indicate that pigeons' ability to recognize stimuli as representatives of real birds depends on the spatial structure of the face stimuli (i.e. the spatial configuration of elements composing the face stimuli), instead of on the single features composing the stimuli.

Moreover, in a subsequent study, the spontaneous reactions of pigeons to images of conspecifics were investigated (Shimizu, 1998). When video images of female pigeons were presented to male pigeons, the duration of males' courtship display was not significantly different from that which they performed in the presence of live females. What is more relevant is that the head region of the video stimuli was more important than the body region in order to elicit courtship behaviour in male pigeons. Thus it seems that also in pigeons the configuration of features present in the head region plays a crucial role in the perception of conspecifics.

However, in another study on pigeons' face perception, Donis, Chase and Heinemann (2005) showed that pigeons were impaired in the recognition of the schematic drawing of a happy *versus* a sad mouth when the mouth was presented within the context of a face with respect to the situation in which the schematic mouths were presented alone. This result seemed to imply that pigeons could not recognize schematic stimuli as faces.

Particular attention should be devoted to the role of eyes, or of features representing the eyes, in face processing in avian species. Eyes are a salient part of the face configuration and they have a predominant role in social interactions (visibility and orientation of the eyes are fundamental signals in order to successfully interact with other animate creatures). Evidence available

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feature seemed to be sufficient for pigeons to discriminate between individual conspecifics and the authors were not able to identify the combination of features required.

in human infant studies suggest that eyes may in fact have a special role in face processing and face preferences (e.g. Easterbrook, Kisilevsky, Hains and Muir, 1999; Farroni, Csibra, Simion and Johnson, 2002; Farroni, Massacesi, Menon and Johnson, 2007; Turati, Valenza, Leo and Simion, 2005. For a review on the role of eyes in directing and causing infants' face preferences and adults' face expertise see Gliga and Csibra, 2007. For evidence of preferential attention to or preferential processing of eyes in primates see also Gothard, Erikson and Amaral, 2004; Gothard, Brooks and Peterson, 2008; Keating and Keating, 1982; 1993; Kendrick, 1991; Kendrick, Atkins, Hinton, Broad, Fabre-Nys and Keverne, 1995; Myowa-Yamakoshi and Tomonaga, 2001b; Myowa-Yamakoshi, Tomonaga, Tanaka and Matsuzawa, 2003; Nahm, Perret, Amaral and Albright, 1997; Tomonaga, 2006. Finally see Lewis and Edmonds, 2003, for evidence of a main role of eyes in adult humans' face detection performance).

Eyes *per se* (independently from recognition of eye-gaze-direction) have been studied mainly as a fear-inducing stimulus for avian species. In fact, conspicuous eyes are a distinctive trait of many potential predators. For example, in humans, the dark spot created by the iris-pupil against the white sclera creates a distinctive luminance pattern characterised by a concentric organization of the two areas having different luminances. The inner area has a lower luminance (i.e. it is darker) than the outer area. A similar pattern is also created by the contrast between the dark pupil and the lighter iris in some avian predators (certain birds of prey species) or non-avian predators (e.g. felines), whereas in other birds of prey (like the peregrine falcon, *Falco peregrinus*), the same perceptive pattern is created by the contrast between the dark eye and the lighter yellowish circle of skin surrounding it. See Figure 5 for images of eyes of different predator species.

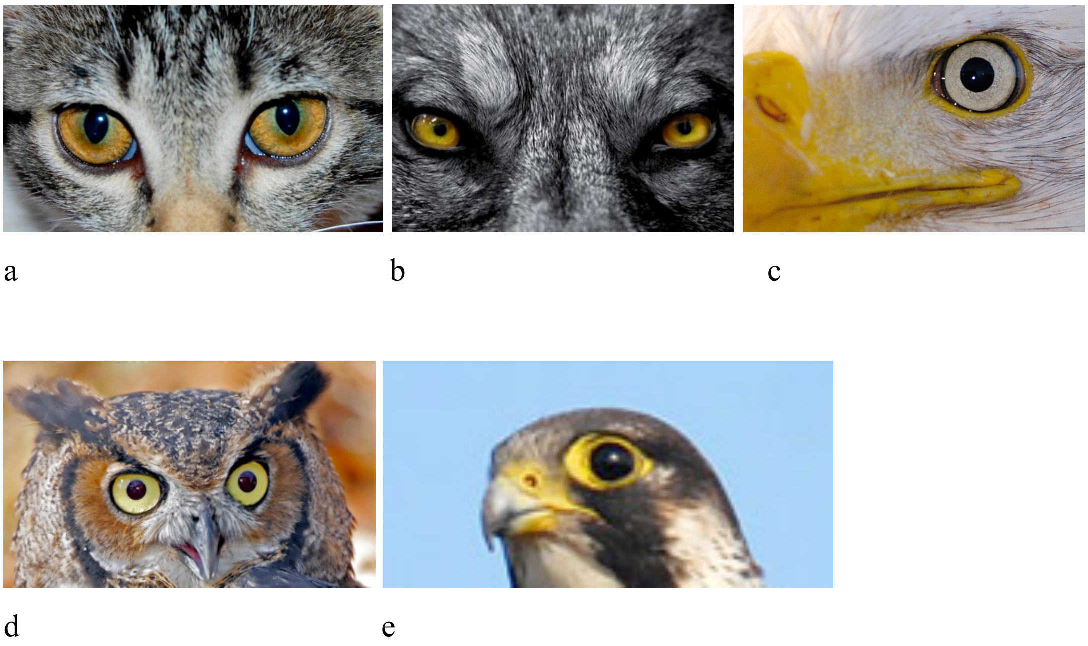

Figure 5
Images of the eye region of different predator species: a) the eyes of a domestic cat (*Felis catus*); b) the eyes of a wolf (*Canis lupus*); c) the eyes of a bald eagle (*Haliaeetus leucocephalus*); d) the eyes of a great horned owl (*Bubo virginianus*); e) the eye region of a peregrine falcon *(Falco peregrinus)*.

As a consequence, schematic eye representations elicit anti-predatory responses in a number of species. Lesser mouse lemurs (*Microcerbus murinus*), jewelfish (*Hemichromis bimaculatus*), wild house mice (*Mus musculus domesticus*), and some birds (including domestic chickens) show this kind of responses that are exploited by some species of butterflies and moths, presenting eye-shaped patterns on their wings (Emery, 2000).

Some interesting studies on this regard have been conducted exploiting domestic chicks' tonic immobility response. Tonic immobility is an innate fear reaction to certain conditions[20] of physical restrain, such as manual capture. This response, which is present in various species[21], consists in a catatonic-

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[20] Responses to a predator could depend on the distance between the predator and the subject. When the predator is distant enough, preys usually freeze. As the distance decrease, preys try to escape or fight, but when there is physical contact and physical restrain, the tonic immobility response occurs: in that way the animal could avoid to be eaten by those predators that eat only live food.

[21] E.g. O'Brien and Dunlap (1975) found that, even in the blue crab (*Callinectes sapidus)*, the tonic immobility duration was increased by manipulations directly relevant to predation fear (like the presence of predators-like glass eyes). Death feigning is a response similar to tonic immobility that was observed in hog-nosed snakes *(Heterodon platyrhinos)*, which react in that way to the presence of eyes oriented

like state of physical immobility and muscle hypertonicity and has probably evolved as a reaction to predation. It has been demonstrated that, in the presence of a dummy predator (a stuffed hawk), the length of few-day-old chicks' tonic immobility response was increased. This effect was made to disappear by covering the hawk's head or just it's eyes (Gallup, Nash, Donegan and McClure, 1971). Similarly, Scaife (1976) demonstrated that chickens' avoidance of a dummy hawk was diminished by obscuring its eyes. Also starlings (*Sturnus vulgaris*) showed a more pronounced fear response when the eyes of a human experimenter were visible than when they were covered (Carter, Lyons, Cole and Goldsmith, 2008). Gallup, Nash and Ellison, (1971) found that the presence of a pair of eyes *per se* (in the absence of any dummy predator containing them) is actually sufficient to increase the duration of tonic immobility in domestic chickens. Yellow eyes seemed to be more effective than brown ones. Gagliardi, Gallup and Boren (1976) found evidence that one specific pupil-size-to-eye ratio (i.e. 11/20) was the most effective in increasing tonic immobility response duration in chickens. It is interesting to note that the eyespots presented by some moths often show the same proportion of 11/20 between the two circumferences composing them. A study by Jones (1980) further investigated which features of two dimensional eye-shapes elicited avoidance in 1-week old chicks, demonstrating an important role of factors such as horizontal orientation (presence of two eyes aligned on the same horizontal line instead of aligned on a vertical line), pairedness of the eyes (presence of 2 eyes instead of 3 eyes or 1 eye) and presence of both iris and pupil. Similarly, sparrows -*Passer domesticus*- reacted more strongly to the presence of 2 eyes than of 1 eye (Hampton, 1994).

Consistent with evidence of the role of eyes as an aversive stimulus, some studies have investigated the ability of avian species (including domestic chickens) to process eye-gaze of a potential predator, demonstrating the presence of a stronger avoidance or fear reaction if the predator's gaze was directed toward the subject or its' nest (Gallup, Cummings and Nash, 1972; Jaime, Lopez and Lickliter, 2009; Watve, Thakar, Puntambekar, Shaikh, Vaze, Jog and Paranjape, 2002; Hampton, 1994; see Emery, 2000 for a review). In

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toward of them. This response is elicited particularly if a human experimenter (that is generally treated as a predator) directs his gaze toward of the snake (see Emery, 2000 for a review).

some cases this ability was also demonstrated when the eye gaze was defined by the position of the eyes only (no head orientation involved) (Carter, Lyons, Cole and Goldsmith, 2008; Rosa Salva, Regolin and Vallortigara, 2007). It is interesting to note that in a recent work conducted in our laboratory we observed a fear reaction to the direct gaze of a potential predator in naïve chicks (Rosa Salva, Regolin and Vallortigara, 2007). However, a subsequent study conducted testing quail (*Colinus virginia*nus) chicks' sensitivity to the gaze direction of a human face, demonstrated that, even though quails were sensitive to gaze direction very early during development, this sensitivity might result as an effect of previous visual experience with human gaze (Jamie, Lopez and Lickliter, 2009).

Although it has been hypothesised that an increased reliance on social signals such as eye gaze would be typical of primates (Emery, 2000), some evidence for the presence of the ability to process eye-gaze in a social context exists also for avian species[22]. For example, hand raised ravens (*Corvus corax*) have been demonstrated to be able to follow the gaze direction of a human being (defined by movement and orientation of both eyes and head), starting from the first months of age (Bugnyar, Stowe and Heinrich, 2004; Schloegl, Kotrschal and Bugnyar, 2007). However, ravens do not seem to be able to use human gaze direction to locate a food reward in an object choice task (Schloegl, Kotrschal and Bugnyar, 2008).

For the experiments that I conducted and that will be described in this thesis, we decided to employ the domestic chick (*Gallus gallus domesticus*) as an animal experimental model to investigate face perception. In the following paragraphs I will thus concentrate mainly on reviewing evidence available with regard to this animal species.

### Presence of an unlearned representation of social objects in chicks

Importantly for the purposes of the present work, domestic chicks (*Gallus gallus domesticus*) have shown evidence of having an unlearned representation of the appearance of a social object. By social object it is here

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[22] However, research on eye-gaze role in guiding social interactions mainly concentrated on primates or few domesticated animals such as dogs (see Emery, 2000).

meant an animate creature regardless of species. Specifically, this definition mainly refers to vertebrates, whose overall physical external structure shares many common traits, recognizable despite the obvious differences between species.

The domestic chick has been widely employed for the study of the neural basis of a conspicuous social phenomenon, known as filial imprinting. This line of research led the identification of specific cerebral areas in the avian brain involved in this form of learning (for a review see Horn and Johnson, 1989; Horn, 2004).

Moreover, it has been theorized (Vallortigara, 1994, pages 61-73) that two different learning processes (possibly associated to different neural substrates) could be comprised in what we usually define simply as imprinting. There could be thus more complexity than usually thought in the formation of memory for the various features of the imprinting object. According to this hypothesis one process would encode the individual features of the imprinting object, allowing the recognition of one particular conspecific with respect to others. On the other hand, another process would encode the invariant features common to all conspecifics, enriching a broad innate representation of the appearance of social partners (or animate objects).

The presence of an innate representation of the appearance of a social object in the chick has been proposed on the basis of the evidence of a predisposition for approaching and imprint on naturalistic (hen-like) objects with respect to artificial stimuli.

For example, imprinting results reversible after the exposition to a second object, if the first and the second objects to which the young animal is exposed are either both naturalistic hen-like objects (live or stuffed hens, Kent, 1987) or both artificial objects (Cherfas and Trooster, 1980; Salzen and Meyer, 1967). The same is true if the first object to which the chick is exposed is an artificial object followed by the exposure to a hen-like object (Bolhuis and Trooster, 1988). On the contrary, a chick who has been imprinted on a stimulus resembling one hen, will not shift its preference toward an artificial object to which it is exposed afterward (Bolhuis and Trooster, 1988; Boakes and Panter, 1985). Evidence is there in the literature suggesting that this asymmetrical reversibility of imprinting preferences could be related to the strength of the initial preference (the more attractive the first object to which the chick is exposed, the more difficult to reverse its preference Salzen and Meyer 1967; Scott, 1980, in Bolhuis and Trooster, 1988). Nevertheless, Bolhuis and Trooster (1988) were able to exclude an interpretation of their results in terms of differential strength of initial imprinting by manipulating the attractiveness of the artificial stimulus they employed (this was done by changing its illumination). In fact, even when the initial preference displayed for the artificial stimulus (by chicks imprinted on it) is stronger than the preference displayed for the stuffed hen (by chicks imprinted on the hen), imprinting results reversible for the chicks exposed to the artificial object first, but not for the chicks exposed to the hen first. The interpretation favoured by these authors (Bolhuis and Trooster, 1988) is thus that the differential reversibility of filial preferences would be due to the interaction of two independent mechanisms: the learning process of imprinting and a predisposition to approach hen-like objects that emerges in the first days of life (see below).

More direct evidence in favour of the presence of an innate representation for the appearance of conspecifics comes from studies proving that domestic chicks spontaneously prefer to approach a naturalistic hen-like object (e.g. a stuffed hen) with respect to an artificial stimulus (e.g. Johnson and Horn, 1986; 1988; Johnson, Bolhuis and Horn, 1985). Some groundbreaking experiments conducted in the '80 showed that, contrary to widely held beliefs, filial imprinting seems to consist of two separate processes. The first process would be an inborn predisposition of the young bird to attend to visual stimuli that resemble a conspecific, such as a stuffed jungle fowl (or even another animal). This predisposition would be based mainly on a broad representation of conspecifics' head appearance. The second process would be a learning mechanism, whereby the chick learns by exposure to recognise the specific characteristics of its own mother hen (guided by the innate predisposition to attend to hen-like stimuli).

Johnson, Bolhuis and Horn (1985) tested naïve newborn chicks 2h or 24h after the exposure to a salient object that was either a red box or a stuffed jungle fowl (the wild ancestor of domestic chicks, Zeuner, 1963). The procedure employed to test chicks' preferences was a simultaneous choice test involving these two stimuli. As expected, 2h after training chicks showed a preference to approach the object to which they were exposed. However, 24h after training chicks had developed a stronger preference for the jungle fowl with respect to the preference that was observed 2h after training, regardless of which was the object to which chicks had been initially exposed. That is to say that, in both chicks trained with the red box and chicks trained with the stuffed jungle fowl, the level of preference for the stuffed fowl increased between 2h and 24h after the initial training. Therefore, chicks initially exposed to the red box, which 2h after training showed a preference for approaching the box, 24h after training performed at chance level, showing no preference for one of the two stimuli. On the contrary, chicks that were initially exposed to the fowl showed a preference for the fowl both 2h and 24h after training. Moreover, also in fowl exposed chicks, the degree of preference for the fowl increased between 2h and 24h after training.

Moreover, the exposure to a complex object was not necessary in order to observe the increased preference for the jungle fowl: the same effect was in fact observed also in chicks that were only exposed to a general (non-specific) motor and visual stimulation. That is to say that this effect was observed also in chicks that were simply placed in a running wheel and exposed to diffuse light (while light exposure alone was not enough) (Johnson, Bolhuis and Horn, 1985). Bolhuis, Johnson and Horn (1985), using a similar procedure, confirmed that motor activity is *per se* sufficient to elicit, after 24h, a significant preference for the stuffed jungle fowl (even in the absence of any prior visual experience). On the contrary, 2h after motor activity, the significant preference for the fowl can be observed only in chicks that have been exposed to a complex abstract visual pattern during the motor activity. It seems thus that structured (but non-specific) visual experience can accelerate the emergence of the predisposition toward hen-like objects. It has to be noticed that the visual input sufficient to accelerate the emergence of the preference for the fowl was an abstract pattern that had nothing in common with the fowl's appearance. The authors of this study (Johnson, Bolhuis and Horn, 1985) claim that the factors inducing or facilitating the emergence of the preference for the fowl (motor activity and non-specific visual stimulation) may act through some physiological processes that would "validate" the system supporting the predisposition to approach the fowl. In line with some literature suggesting a role of plasma level of testosterone in determining the expression of chicks' preferences (see below), it has been suggested that these critical experiences would influence the plasma level of testosterone. Other non-specific experiences that allow the emergence of the predisposition to approach the fowl are handling of chicks and exposure of chicks to a maternal call (Hampton, Bolhuis and Horn, 1995). The non-specific experience, in order to be effective in inducing the emergence of the predisposition, has however to be provided during an appropriate sensitive period (Johnson, Davies and Horn, 1989; Davies, Johnson and Horn, 1992; Bolhuis and Horn, 1997; Bolhuis, Johnson and Horn, 1989).

In 1988 Johnson and Horn investigated the nature of the hypothesised representation of animate objects' appearance that would underlie the above-described results. The authors wanted to investigate the role of some properties that differ between hen-like and artificial objects, such as stimulus complexity (ad more specifically outline complexity or textural complexity) or specific configurations of stimulus' feature clusters. In order to do so, spontaneous preferences for pairs of stimuli were tested in naïve chicks 2h and 24h after motor activity (no visual experience whatsoever was allowed prior to test time). In the first experiment chicks' preferences were compared between a stuffed fowl and an artificial stimulus (a red box) whose level of complexity was manipulated (by adding black stripes to its surface). Results showed that, if anything, chicks preferred the fowl more strongly when it was compared with a complex rather than a simple red box. In Experiment 2, an intact stuffed fowl was compared to scrambled fowls, in order to rule out some of the fowl's visual features as responsible for chicks' preferences. For a reproduction of some of the scrambled hens used as control stimuli by Johnson and Horn (1988) see Figure 6.

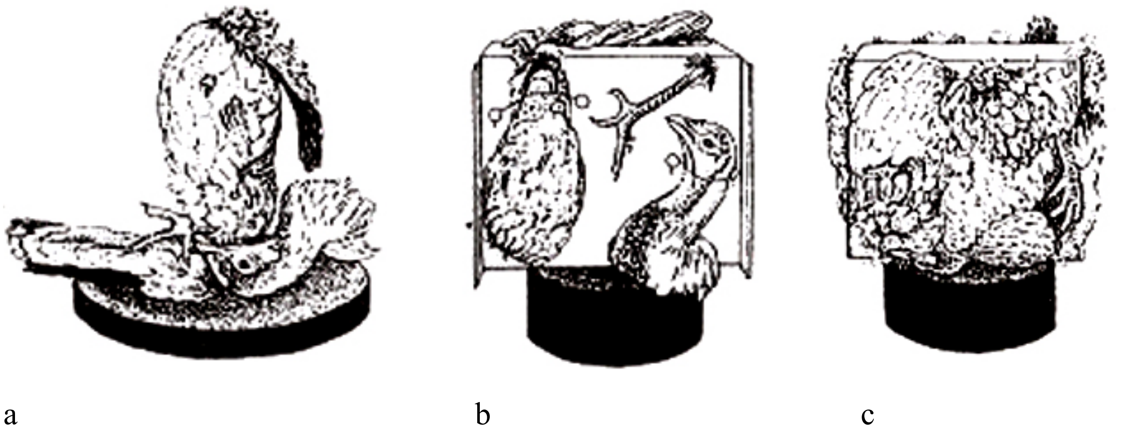

Figure 6
Reproductions of the scrambled hens used as control stimuli by Johnson and Horn (1988). Stimulus a) is a severely scrambled fowl, whose body parts were reassembled in anatomically unusual ways. Stimulus b) is a box-fowl whose body parts were mounted on the sides of a box, so that the outline of the stimulus was that of a box. Stimulus c) is a texture-fowl, obtained by cutting up in small pieces the trunk pelt of a jungle fowl and attaching them to the sides of a box in scrambled positions, together with other body parts of the fowl.

Control stimuli used for this experiment were: moderately and severely disarticulate fowls (whose limbs and body parts were reassembled in anatomically unusual ways, maintaining on the other hand the outline complexity typical of the fowl); a box-fowl (limbs and body parts of the fowl were mounted on the sides of the box, so that the outline of the stimulus was that of a box, but all body elements of a fowl were visible and intact); a texture-fowl (the trunk pelt of a jungle fowl cut up in small squares and attached to the sides of the box in scrambled positions together with other body parts of the fowl; in this stimulus the single features of the fowl were still present, as well as its textural complexity, but spatial relationships between single features were altered, i.e. few if any of the natural cluster of features of the fowl were maintained by the stimulus). The intact fowl was preferred only with respect to this last control stimulus, showing that neither anatomical plausibility, nor outline complexity or textural cues could be at the basis of chicks' preferences.

It seems thus that chicks were responding to the presence of some spatial relationship among natural clusters of features that was abolished in the texture-fowl control stimulus. In order to investigate to which cluster or configuration of fowl's features chicks may respond, in Experiment 3 the authors compared chicks' preferences for the intact fowl to their preferences for the head and neck region of a fowl mounted on a box. No preference was observed between the two stimuli, implying that the configuration of features contained in the head and neck alone are at least as attractive to the chick as the whole fowl. Moreover, the magnitude of the preference for the intact fowl was smaller in Experiment 3 than in all other experiments (thus the stimulus comprising the neck-head alone was the "more preferred" control stimulus). This was interpreted by the authors as a sign that elements outside the neck-head region could act as distractors, weakening chicks preferences. In Experiments 4 and 5 the authors assed the species-specificity of chicks' preferences by presenting the birds with the choice between a stuffed fowl and a stuffed duck or polecat (a mammal and a potential predator to chicks). Chicks did not show any preference for the fowl in none of the two cases (for similar evidence of non-species specific preferences in chicks see also Gray, Yates, Sallee and Gray, 1980). In summary, the representation of the appearance of a social object that underlies chicks' preferences seems to be based on some cluster or configuration of features, likely contained in the neck-head region, and it seems also to be extremely broad, so broad to be even not species specific[23]. In order to be preferred by chicks, it is only needed

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[23] The presence of social predispositions that are not species specific (i.e. not limited to the species to which the animal belongs to) has been supported by evidence obtained in different kinds of studies. Evidence of non-species-specific predispositions present in chicks prior to any visual experience emerged also in some works on sensitivity to biological motion (Vallortigara, Regolin and Marconato, 2005). Similar evidence for a non-species-specific preference for biological motion was also obtained in human newborns (Simion, Regolin and Bulf, 2008). As regards face perception, in the absence of extensive visual experience with faces, monkeys showed a preference for faces with respect to other objects that was not species specific (i.e. human faces and monkey faces were equally preferred) (Sugita, 2008). Similarly, Tomonaga (2006) demonstrated in chimpanzees a non-species-specific detection advantage for upright faces that could be elicited by dog faces or schematic drawings (however, literature on the species specificity of primates' face processing is still controversial). Consistent with the evidence described here for primates is the fact that the *other species effect* (better processing in humans of human faces than of other primates' faces) seems to be absent in babies up to 6 months of

that a stimulus posses a head with face inner features in the correct relative locations (regardless of whether these features belong to a bird face or not) and a neck. The main role of the neck-head region in chicks' preferences makes sense also in the context of the ecological niche of this species: in fact combination of features of the head are particularly important in the recognition of other individuals in adult chickens (Candland, 1969; Guhl and Ortman, 1953).

This pattern of results presents a striking resemblance with what previously described for human newborns, whose preferences have been supposed to be driven by the presence of a triangular arrangement of highly schematic internal features (black blobs) in the appropriate location for eyes and mouth (i.e. with one vertex of the triangle pointing down), within a face-like outline (Morton and Johnson, 1991). It is relevant to note that the very same representation of face's structure that Mark Johnson hypothesised to be at the basis of newborns' face preferences (Morton and Johnson, 1991; Johnson, 2005), could also induce the preference for naturalistic objects' demonstrated in chicks. In fact, a hen's or a chick's face, when observed in a frontal view and under natural top-lit illumination, present exactly the same triangular configuration of darker areas on a lighter background as hypothesised by Johnson in his CONSPEC-CONLERN model. See Figure 7.

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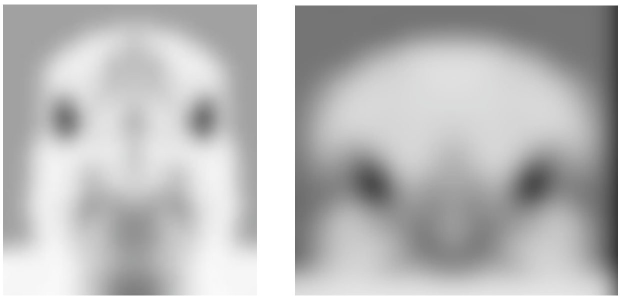
age. This suggests that initial face preferences would be non-species-specific and would become selective for human faces only after extensive experience with this stimulus (Pascalis, de Haan and Nelson, 2002). Finally, it is curious to note that infants' preferences for attractive faces seem to apply also to faces of other species (Quinn, Kelly, Lee, Pascalis and Slater, 2008).



a b

Figure 7
Images shown were obtained in order to illustrate that a hen’s face (a) and a chick’s face (b) seen from a frontal view under top-lit illumination present a triangular configuration of dark areas (the two eyes and the shadowed area under/around the bill). Notice that both the mother hen and sibling chicks can become the imprinting object of a newborn chick in the natural environment. To create the images, photographs of a hen’s face and of a chick’s face were filtered employing the contrast-increase and blurring functions of the Photoshop 6.0 software program (Adobe Systems, Inc., Mountain View, California, USA).

It seems also that the neural basis of the innate representation of a social object that chicks have is not the same as that described for imprinting: the preference for hen-like objects is not suppressed by bilateral lesions of the area involved in imprinting (Intermediate Medial Mesopallium, IMM, Horn and McCabe, 1984; Johnson and Horn, 1986). In fact, lesioned chicks fail to show any preference for the object to which they have been exposed during training (as expected after an IMM lesion), but still develop an increasing predisposition for the stuffed fowl 24h after training. Moreover Davies, Horn and McCabe (1985) demonstrated that the injection of the noradrenaline neurotoxine DSP4 (that reduces noradrenaline concentration) strongly impairs preference for an artificial imprinting object[24], whereas it has little or no effect on preferences for a stuffed fowl. The forebrain concentration of noradrenaline also correlates with the strength of imprinting for the artificial object (but not with the level of

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[24] Authors predicted the effect of DSP4 in chicks exposed to an artificial imprinting object on the basis of the hypothesis that noradrenaline may influence learning through a primary effect on synapses (Kety, 1972; Crow and Arbuthnott, 1972). Moreover, noradrenaline is present in the chick forebrain and its concentration increases after exposure to the imprinting object (Davies, Horn and McCabe, 1983).

preference for the stuffed fowl) (but see Davies, Johnson and Horn, 1992, for the role of DSP4 in delaying the onset of the sensitive period during which non-specific experience is effective in eliciting the spontaneous preference for hen-like stimuli). On the other hand, in a similar experiment, Bolhuis, McCabe and Horn (1986) demonstrated that the administration of exogenous testosterone increased the preference for the imprinting stimulus in chicks exposed to the stuffed fowl but not in chicks exposed to an artificial stimulus. Similarly, plasma testosterone concentration correlated with the level of preference for the fowl, but not with that for the artificial stimulus. Finally, Payne and Horn (1984), recording the spontaneous activity of IMM neurons in anaesthetised chicks that had been imprinted either on the stuffed fowl or on an artificial stimulus, demonstrated a negative correlation between spontaneous IMM impulse activity and approach counts during exposure to the imprinting stimulus only in fowl-imprinted chicks. In favour of the presence of two independent mechanisms at the basis of imprinting and of spontaneous preferences is also the fact that the emergence of the predisposition to approach hen-like objects does not prevent chicks from learning features of artificial objects to which they are exposed (Bolhuis, Johnson and Horn, 1989).

Thus, it has been suggested (Johnson, 1992; Morton and Johnson, 1991) that the CONSPEC-CONLERN model hypothesising the presence of two independent mechanisms underlying babies' preferences for faces, could apply also to filial imprinting in chicks and to chicks' preferences for hen-like stimuli. According to that view, chicks would have two distinct neural systems. One would be in charge of a predisposition to attend to objects resembling conspecifics (CONSPEC) on the basis of an innate representation of their appearance (especially that of the structure of their faces) and would orient the chick's attention toward stimuli that match this representation, in the absence of any prior experience. The other mechanism (CONLERN) would be a learning device, in charge of memorizing the features of the objects toward which CONSPEC orients the animal's attention. In this way chicks would learn to recognize individual features of a certain conspecific that will become their imprinting object, developing a recognition memory for a certain hen or chick.

A neural network model of the interactions between filial imprinting and the spontaneous preference for heads and necks has also been developed in recent years. The model, which hypothesised different “neural substrates” for the predisposition and for the imprinting process, was based on a genetic algorithm simulation (emphasizing the survival value of innate and learned information). This model was proved able to reproduce the actual behaviours exhibited by chicks in some experiments on imprinting and filial preferences (Hadden, 2002).

It is finally worth noting that evidence of the presence of an innate representation for the appearance of animate objects was obtained also in studies that investigated spontaneous preferences for point light displays representing biological motion in visually naïve chicks (Vallortigara, Regolin and Marconato, 2005; Vallortigara and Regolin, 2006; Troje and Westhoff, 2006; Johnson, 2006). For similar evidence in newborn babies see Simion, Regolin and Bulf (2008). Thus, it seems that chicks could be endowed with a set of multiple mechanisms enabling them to locate appropriate social objects in the absence of any prior visual experience. These mechanisms would however be based on very broad representations, resulting in preferences that are not species specific. In fact a point light display representing the movement pattern of a walking hen is not preferred by chicks over a point light display representing the movement pattern of a walking cat (Vallortigara, Regolin and Marconato, 2005). This result presents a striking resemblance with the evidence reported by Johnson and Horn (1988), showing that chicks do not prefer to approach a stuffed hen with respect to a stuffed polecat.

The presence of converging evidence on non-species-specific animacy detection devices in newborn babies, whom show a preference for looking at a point light display of a walking hen (Simion, Regolin and Bulf, 2008), stresses the remarkable similarities among the mechanisms demonstrated in chicks and human babies. A further source of analogies between the two species is the presence, in both human newborns’ and domestic chicks, of an early sensitivity to gaze direction (Farroni, Csibra, Simion and Johnson, 2002; Rosa Salva, Regolin and Vallortigara, 2007). When considering the convergence of results between domestic chicks and human babies it appears thus that the domestic chick provides an advantageous animal model to investigate issues emerging from the developmental literature.

The advantages of the use of domestic chicks will be described in the following paragraph, but it is worth noting that in the above mentioned papers (e.g. Vallortigara, Regolin and Marconato, 2005; Rosa Salva, Regolin and Vallortigara, 2007) the use of visually deprived chicks had the advantage of providing us with clear cut evidence of experience independent predispositions. On the contrary, previous experience with relevant stimuli is a confounding factor impossible to rule out in developmental studies on human babies (such a confounding factor may be also difficult to control in studies on other primate species).

## The domestic chick as an animal experimental model

Chicks offer several advantages as an animal model for behavioural experiments.

First of all, the *Gallus gallus domesticus* is a precocial species: chicks hatch in an advanced state of development and are able to feed almost immediately. This allows to test animals only few days or even hours after hatching, obtaining a nearly complete control over the subjects' previous experience. The use of the chick has also practical advantages: it is an animal easy to obtain, inexpensive, and its neuroanatomy and neusophysiology are very well known with respect to other species. Moreover, chicks' behavioural responses are discrete and easy to detect, making the behavioural measures more objective.

Young chicks are also endowed with remarkable cognitive abilities, especially concerning learning skills, such as the perceptual learning involved in filial imprinting.

In addition, another advantage of this species is that chicks present a very well developed vision (Schmid and Wildsoet, 1998). Moreover, this species also present a difference in visual acuity in the upper visual field with respect to the lower one (Hodos and Erichsen, 1990). This is especially relevant because it has been hypothesised that a different visual sensitivity in the upper or lower visual field could be an important factor underlying human newborns' face preferences (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002; see also the paragraph "Introduction to

Experiments 1-4: Role of vertical asymmetry of inner facial elements in face preferences ”).

Moreover, homologies of brain structures between avian and mammalian species have been increasingly recognized in recent years (Jarvis et al., 2005). While, the traditional view held that the avian cerebrum is almost entirely composed of the basal ganglia, recent evidence suggest that the avian cerebrum has a large pallial territory that performs functions similar to those of the mammalian neocortex. Despite the profound structural differences (the avian pallium is nuclear, and the mammalian neocortex is laminar in organisation), the avian pallium is homologous to the mammal cortex and supports similar functions.

Many parallels exist between domestic chicks’ and mammals’ social cognition, some of which have been described in the above paragraphs. Chicks in fact are a highly social species, whose members need to be able to recognize individual identity and do so by using features present in the head and neck region (Candland, 1969; Guhl and Ortmann, 1953). Moreover, chicks seem to be endowed with a certain number of early mechanisms that direct their attention toward conspecifics and other animate objects, and in particular toward relevant aspects of others’ behaviour (social cues). Those mechanisms include a sensitivity to biological motion (Vallortigara, Regolin and Marconato, 2005; Vallortigara and Regolin, 2006) and gaze direction (Rosa Salva, Regolin and Vallortigara, 2007) and a general predisposition to approach objects that look like the head of a vertebrate animal (e.g. Johnson and Horn, 1988). Those predispositions present a striking resemblance with those observed in human newborn babies (Farroni, Csibra, Simion and Johnson, 2002; Morton and Johnson, 1991; Simion, Regolin and Bulf, 2008), making the domestic chick a promising model for the investigation of early social predispositions in vertebrate species.

## Introduction to Experiments 1-4: Role of vertical asymmetry of inner facial elements in face preferences

Within the framework determined by the current debate in the developmental literature between the sensory and the structural hypothesis, and contrary to Morton and Johnson's (1991) theory, it has been claimed that newborns' face preferences could arise as a secondary effect from a number of non-specific attentional biases that would induce a general preference for some structural properties of a visual stimulus. According to this theory, face processing at birth is mediated by general, rather than domain-specific perceptual processes. These non-specific biases could be due to the constraints imposed by the immature visual system of the newborn baby (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002; Simion, Macchi Cassia, Turati and Valenza, 2001). Newborns would thus prefer face-like stimuli not because these possess the unique geometry of a face (*facedness*), but because they possess some more general structural properties (that they share with stimuli other than faces) whose additive effects would determine a visual preference for faces (Macchi Cassia, Valenza, Simion and Leo, 2008; Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002). It seems possible, in fact, to define faces as collections of general structural properties: they are symmetrical along the vertical axis, they present more patterning in the upper than in the lower half, and they have rounded rather than sharp edges (Johnson and Morton, 1991). An advantage of the "general biases" theory is that it allows to combine the structural and sensory hypotheses, thus explaining some results obtained in the literature that still seem to contradict the structural hypothesis in favour of the sensory one (e.g. Easterbrook, Kisilevsky, Hains and Muir, 1999). This would be possible assuming that the visibility of one stimulus (either a face- or a non-face-like one) is determined not only by the amount of energy contained in the pattern, but also by its structural properties (how energy is distributed within the pattern) (Simion, Macchi Cassia, Turati and Valenza, 2001).

This theory is based in the first place on evidence that faces' structural visual properties are capable of producing a preferential response even when they are embedded in non-face stimuli (Macchi Cassia, Valenza, Pividori and Simion, 2002; Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002). In fact, the perception of stimuli other than faces can be influenced by structural properties (Fantz, 1965; Macchi Cassia, Simion, Milani and Umiltà, 2002; Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Slater and Sykes, 1977; Slater, Earle, Morison and Rose, 1985; Farroni, Valenza, Simion and Umiltà, 2000) some of which are shared by faces, suggesting that qualitatively similar perceptual processes could be employed both for perception of faces as well as of other objects.

Much research has focused on the role of one of the structural properties that characterize faces, the up-down asymmetrical distribution of the inner facial features (faces display two features – the eyes – in the upper part and only one feature – the mouth – in the lower part) in determining preference for face-like stimuli. It has been proved (Simion, Valenza, Macchi Cassia, Turati, and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002, Experiment 1) that in human newborns the vertical (up-down) asymmetry in the distribution of internal elements can affect preferences displayed for non-face stimuli: participants looked longer at a non-face stimulus with a greater quantity of high-contrast elements in the upper half (i.e. a top-heavy configuration) than at a non-face stimulus with more patterning in the lower half (i.e. a bottom-heavy configuration). For the stimuli employed by Simion, Valenza, Macchi Cassia, Turati and Umiltà (2002) see Figure 8.

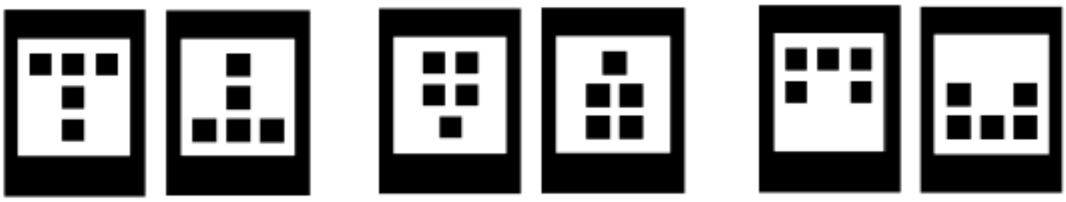

Figure 8
Reproduction of the three pairs of stimuli (pair a, b and c) employed by Simion, Valenza, Macchi Cassia, Turati and Umiltà (2002). Each pair consists in a top-heavy (a1, b1 and c1) and a bottom-heavy (a2, b2 and c2) non-face-like configuration. The bottom-heavy configuration is identical to the top-heavy configuration but rotated of 180°.

The authors of this paper (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002) suggested that the preference for top-heavy stimuli in newborns could derive from an upper versus lower visual field difference in visual sensitivity, similar to that observed in adults, which could render top-heavy patterns more easily detectable for newborns than other stimuli. According to Simion and colleagues "*The fact that the stimulus preferred by the newborns was the one in which more elements were in the upper rather than in the lower part of the configuration might be interpreted as a suggestion for the existence of an upper visual field advantage at birth: newborns might have preferred the pattern in which the more salient part was presented to the more sensitive portion of the visual field. That is, the overall visibility of the pattern with more elements in the upper part might have been improved as a consequence of the greater sensitivity of the upper visual field*" (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002).

It is worth noting that no direct evidence of the presence of such a difference in sensitivity between the upper and the lower visual filed in infants is reported by Simion and her colleagues (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002). In fact, the claims for the presence of a difference in contrast sensitivity between the upper and lower visual field in newborns are based on indirect evidence (i.e. mainly on parallels with evidence obtained in adults). As regards the presence of an upper versus lower visual field difference in visual sensitivity in adults, many studies report a lower rather than an upper visual field advantage[25] (Carrasco, Talgar and Cameron, 2001; Chedru, Leblanc and Lhermitte, 1973; Gawryszewski, Riggio, Rizzolatti and Umiltà, 1987; Jeannerod, Gerin and Pernier, 1968; Payne, 1967; Rijsdijk, Kroon and van der Wildt, 1973; Rizzolatti, Riggio, Dascola and Umiltà, 1987; Rubin, Nakayama and Shapley, 1996; Talgar and Carrasco, 2002; Tychsen and Lisberger, 1986). For example, Rijsdijk, Kroon and van der Wildt (1973) demonstrated a higher contrast sensitivity in the lower-visual filed rather than in the upper-visual filed[26]. Similarly, Rubin, Nakayama and Shapley (1996) demonstrated the presence of a lower visual field advantage in detection of illusory contours. However, they were not able to demonstrate any significant difference between the two hemifields in terms of shape discrimination and orientation discrimination (tasks not influenced by the perception of illusory contours, but by the mere visibility of stimuli). More recently, two studies demonstrated that contrast sensitivity and spatial resolution are higher in the lower than in the upper vertical meridian of our visual field (Carrasco, Talgar and Cameron, 2001; Talgar and Carrasco, 2002) [27].

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[25] However, some studies failed to report any difference between the two visual fileds (e.g. Carrasco, Evert, Chang and Katz, 1995; Carrasco and Frieder, 1997; Carrasco, McLean, Katz and Frieder, 1998).

[26] On the contrary, a shorter latency for saccadic eye movements to static targets in the upper visual field has been demonstrated by Heywood and Churcher (1980). However, conflicting evidence was obtained by Tychsen and Lisberger (1986), who demonstrated larger eye movements acceleration to pursuit targets in the lower visual field. Similarly, latency of manual reaction time seems to reflect a lower visual field advantage in stimulus detection (Payne, 1967; Gawryszewski, Riggio, Rizzolatti and Umiltà, 1987; Rizzolatti, Riggio, Dascola and Umiltà, 1987) and in visual search, which has longer latency and duration in the upper visual field (Chedru, Leblanc and Lhermitte, 1973; Jeannerod, Gerin and Pernier, 1968, *in Simion, Valenza, Macchi Cassia, Turati, and Umiltà, 2002*). Finally, attentional resolution seems to be higher in the lower visual field (He, Cavanagh and Intriligato, 1996).

[27] Talgar and Carrasco (2002) point out that the existence of a difference in spatial resolution between the upper and lower part of the vertical meridian of the human visual field (which they have successfully proved) is not equivalent to an overall difference between all of the possible locations in the upper and lower visual fields. However, according to Talgar and Carrasco, the reported advantage of the lower visual field in psychophysical tasks (see above) might be due to the differences in spatial resolution and contrast sensitivity present along the vertical meridian. Similarly, results obtained in studies that failed to report any lower visual field advantage (Carrasco, Evert, Chang and Katz, 1995; Carrasco and Frieder,

Possibly due to the fact that adult data point toward a lower, rather than an upper, visual field advantage, Simion, Valenza, Macchi Cassia, Turati and Umiltà (2002) recognize that: "*an alternative (and opposite) interpretation* [with respect to their previous interpretation of the up-down bias as due to an upper visual field advantage] *is also tenable. Newborns' preference for the stimulus with more elements in the upper part of the configuration may be indicative of the existence of a lower rather than an upper visual field advantage in visual sensitivity. Newborns might have preferred the stimulus in which the more salient part of the configuration was presented to the less sensitive portion of the visual field. This is because they might have preferred a symmetrical pattern, but the up-down symmetry was achieved on condition that the more salient part of the pattern was presented to the less sensitive upper portion of the visual field*" (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002).

Another potential problem in the interpretation of results obtained in adults is due to the fact that data available in the literature are also controversial as to whether the above mentioned differences between the upper and lower visual fields in adults are due to perceptual or attentional processes (e.g. He, Cavanagh and Intriligator, 1996; Rubin, Nakayama and Shapley, 1996; Rijsdijk, Kroon and van der Wildt, 1973). However, recent studies indicate that visual rather than attentional factors are likely to be responsible for the asymmetry in contrast sensitivity and spatial resolution observed along the vertical meridian of our visual field (Carrasco, Talgar and Cameron, 2001; Talgar and Carrasco, 2002).

In consideration of the indirect nature of the evidence supporting the interpretation of their results put forward by Simion, Valenza, Macchi Cassia, Turati and Umiltà (2002), and in consideration of the multiple and conflicting interpretations proposed by these authors (see above), the possibility that the source of the up-down bias in newborns is a difference of sensitivity between the upper and lower halves of the visual fields should be considered with caution.

Interestingly, it seems to be possible that also face recognition would be biased toward the upper visual field: upper facial features could be more critical than

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1997; Carrasco, McLean, Katz and Frieder, 1998), may be due to the fact that averaging performance across several locations could obscure the real differences present along the vertical meridian.

lower ones in face recognition (Sheperd, Davies and Ellis, 1981, *in Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002*).

On the basis of the above discussed evidence it has been hypothesised that the same factor (i.e. the differential sensitivity of the two visual hemi-fields) could play a crucial role in determining newborns' preference for faces. The presence of an upper visual field advantage in newborns, such as that hypothesised by Simion, Valenza, Macchi Cassia, Turati and Umiltà (2002), would also be consistent with the fact that the superior colliculus, that strongly affects newborns' visual behaviour (Atkinson, Hood, Wattam-Bell and Braddick, 1992; Braddick, Atkinson, Hood, Harkness, Jackson and Vargha-Cadem, 1992; Johnson, 1990), plays a major role in visual exploration toward the upper visual field (Sprague, Berlucchi and Rizzolati, 1973, *in Turati, Simion, Milani and Umiltà, 2002*).

In indirect support of the hypothesis that top-heaviness is a relevant factor for newborns' face preferences, there are some findings showing that a schematic face-like stimulus containing only some of the features located in the upper part of the face (i.e. the eyes) was similarly preferred with respect to a whole schematic face (Easterbrook, Kisilevsky, Hains and Muir, 1999). For stimuli employed by Easterbrook and colleagues (1999), see Figure 9.

a b

Figure 9

Reproduction of two of the stimuli employed by Easterbrook, Kisilevsky, Hains and Muir (1999). Stimulus a) represents the schematic drawing of a face, complete with all the face features; stimulus b) represents the same face outline but containing only the eyes.

It should be noticed, however, that this result could also be easily explained in terms of a greater importance for social communication of the eyes with respect to other face traits (as it has been suggested by some recent models that assume that the detection of potentially communicative partners could be a major function of newborns' face preferences, Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005; Johnson, 2005).

However, the strongest evidence in favour of the up-down bias hypothesis, comes from an innovative work of Turati, Simion, Milani and Umiltà (2002), who replicated the findings of Simion, Valenza, Macchi Cassia, Turati and Umiltà (2002), demonstrating that human newborns prefer to look at a top-heavy over a bottom-heavy non-face-like configuration (Experiment 1, Figure 10, a1, a2). Even more relevantly, the same study provided evidence that a face-like configuration is not preferred by newborns over another top-heavy configuration that presents a non face-like arrangement of inner features (Experiment 2, Figure 10, b1, b2). Moreover, a non face-like top-heavy configuration was preferred over a face-like bottom heavy stimulus (Experiment 3, Figure 10, c1, c2).

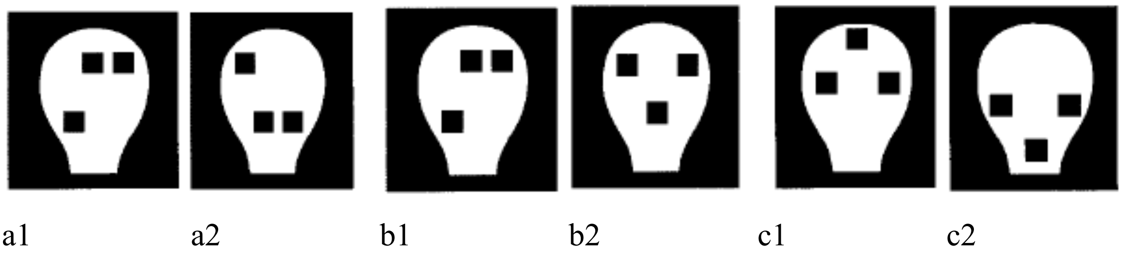


Figure 10

The three pairs of stimuli employed by Turati, Simion, Milani and Umiltà (2002) in Experiment 1 (a1, a2), Experiment 2 (b1, b2) and Experiment 3 (c1, c2). Stimuli consist in non-face-like top-heavy configurations (a1, b1, c1), a non-face-like bottom-heavy configuration (a2), a face-like top-heavy configuration (b2) and a face-like bottom-heavy configuration (c2).

According to these results it seems that newborns' preference for face-like stimuli could just arise as a secondary effect of a more general preference for top heavy-configurations, determined by the constrains of the immature visual system of the newborn. Not denying the extreme relevance of the results obtained by Turati, Simion, Milani and Umiltà (2002) for this field of research, it is worth to point out that there could be some methodological issues related to this work, mainly concerning the experimental stimuli employed, that should be considered when interpreting the results obtained. It should be noticed in fact that, when comparing newborns' preference for a face-like with respect to a non-face-like top-heavy configuration (Experiment 2), Turati and others employed a couple of stimuli which did not differ only in their *facedness* (disposition of inner features according to the overall configuration of a face) but also in their symmetry. In fact, the face-like stimulus was symmetrical on the vertical axis, whereas the non-face like-stimulus was asymmetrical on this dimension. As symmetry is another relevant structural property of a stimulus, it is possible to hypothesise that this could have influenced newborns' responses in Experiment 2. However, in this case, the most obvious hypothesis is that newborns should prefer the symmetrical face-like stimulus. On the contrary Turati and colleagues did not observe such a preference, in line with what predicted by the up-down bias theory. Thus, at first sight, it seems that the results obtained by Turati and colleagues in Experiment 2 can not be explained as due to the fact that stimuli were not balanced in terms of symmetry. Nevertheless, since symmetry is an important structural property of a stimulus, it is also possible to hypothesize that the processing of asymmetrical stimuli could be more difficult than that of symmetrical ones and could require additional attentional resources (Bornstein, Ferdinandsen and Gross, 1981; Fisher, Ferdinandsen and Bornstein, 1981). Therefore, in future studies aimed at investigating this topic, it could be interesting to employ stimuli that are controlled for their symmetry.

As regards the third experiment conducted by the authors, it should be noticed that the face-like configuration employed had its inner features located in a very low position within the face outline, and thus its resemblance with the face of an adult human being (the most likely caregiver of the newborn) is quite reduced. This could have affected the recognition of such a stimulus as a face by the newborns (there are, in fact, some evidence suggesting that the spatial relationship between the inner configuration of features and the face contour is relevant in determining a preference for faces, Simion, Valenza, Umiltà and Dalla Barba, 1998; Turati, 2004; see also Johnson, 2005 for a review).

Part of the results of obtained by Turati, Simion, Milani and Umiltà (2002) have been recently confirmed using more naturalistic stimuli (natural and scrambled photographic images of real faces), displaying the same structural properties as those employed by Turati and colleagues (Macchi Cassia, Turati and Simion, 2004). Results obtained in this study demonstrated that human newborns show a visual preference for a normal face with respect to a face whose inner features have been rotated of 180° within the face outline (Figure 11, Experiment 1), that they prefer to look at a top-heavy scrambled face with respect to a bottom heavy scrambled one (Figure 11, Experiment 2, confirming the results of the first experiment of Turati Simion, Milani and Umiltà, 2002) and that they do not show any preference for a normal face with respect to a scrambled but still top-heavy face (Figure 11, Experiment 3, confirming the results of the second experiment of Turati, Simion, Milani and Umiltà, 2002). It is worth noting that stimuli employed in Experiment 3 by Macchi Cassia, Turati and Simion (2004) differ in symmetry (the face is symmetrical, but the scrambled face is not), as already pointed out for the corresponding stimuli employed by Turati and her colleagues (2002) in their second experiment (see above). This study also validates the use of schematic stimuli to investigate face preferences, demonstrating that results can be generalized to more ecological stimuli.

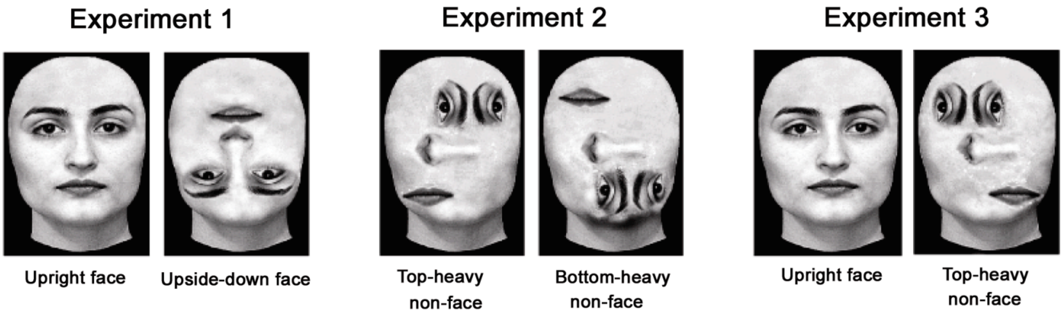
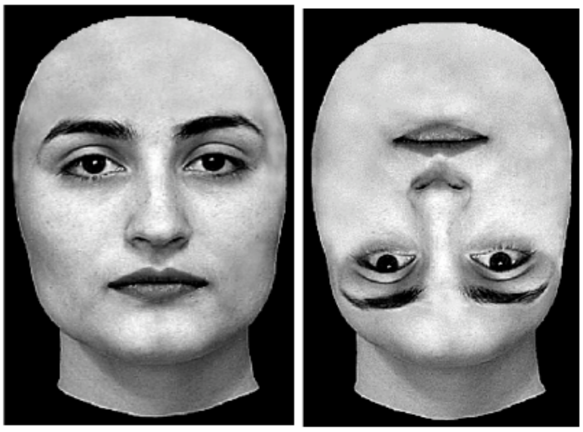


Figure 11

Stimuli employed by Macchi Cassia, Turati and Simion (2004).

More ambiguous evidence was obtained in a further study of the same research group (Turati, Valenza, Leo and Simion, 2005), which investigated the development of the up-down bias and of its relation with face preferences during ontogenesis, by testing 3-month-old babies.

In the first experiment conducted by Turati, Valenza, Leo and Simion (2005) these authors also demonstrated that 3-month-old babies look longer at the photographic image of a normal face (Figure 12a) with respect to that of a face whose inner features have been rotated of 180° within the face outline (Figure 12b) (thus confirming the results already obtained in newborn babies by Macchi Cassia, Turati and Simion, 2004, Experiment 1). Moreover the upper half of the normal face image was looked longer than chance level, whereas the upper half of the upside down face was not.

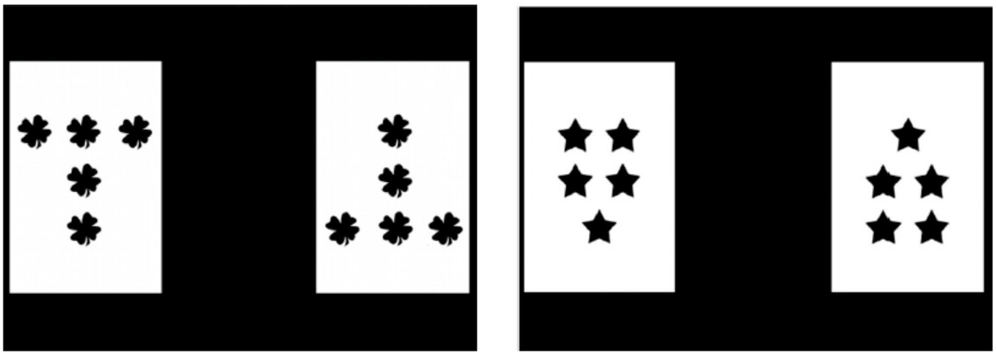


a b

Figure 12

An example of the pairs of stimuli employed by Turati, Valenza, Leo and Simion (2005) in Experiment 1. The stimuli represent a face (a) and an upside-down version of the same stimulus, where the face traits have been rotated of 180° within the face outline to represent a non-face-like bottom-heavy configuration (b).

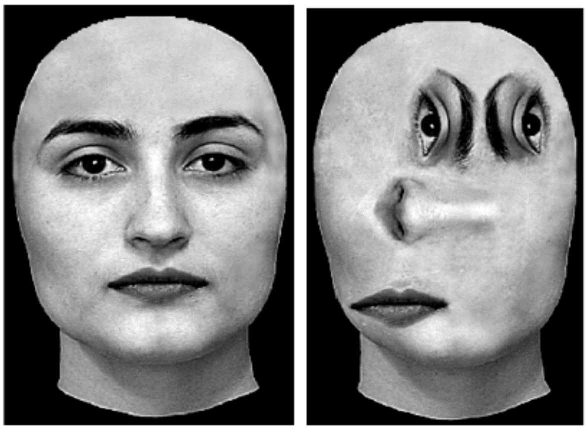
In a second experiment, Turati, Valenza, Leo and Simion (2005) investigated whether 3-month-olds would prefer to look at top-heavy over bottom-heavy configurations as newborns did. According to the results obtained for the overall looking time, 3 month-old babies would still prefer to look at top-heavy geometric non face-like stimuli with respect to bottom-heavy ones, but contrary to newborn babies they would do so only when the up-down asymmetry is highly salient (Experiment 2, Figure 13, b1-b2). In fact, according to the authors of this study, 3-month-old infants show a preference for the top-heavy stimulus when the difference between the upper and lower part of the image in terms of the number of inner elements is highly marked, as in Figure 13, b1-b2, but not in Figure 13, a1-a2. However, results obtained for the distribution of looking time across the figure surface showed that the upper portion of the top-heavy patterns was looked significantly more than chance lever (regardless of the pair of stimuli employed). On the contrary, the lower part of the bottom heavy stimulus was observed as predicted by chance level. Thus, it seems that the preference for top-heavy configurations would be weaker, but still present, at 3 months of age: the up-down bias would not disappear abruptly during ontogenesis, but rather would do so progressively.



a1 a2 b1 b2

Figure 13
An example of the pairs of stimuli employed by Turati, Valenza, Leo and Simion (2005) in Experiment 2. The stimuli represent two top-heavy configurations (a1, b1) and two bottom-heavy configurations (a2, b2). In stimuli a1-2 the difference in the number of elements present in the upper and lower part of the configurations has been claimed to be less marked than in stimuli b1-2. In fact, according to the description of stimuli given by the authors themselves, stimulus a1 presents 3 elements in the upper part of the configuration and 2 in the lower part, whereas stimulus b1 presents 4 elements in the upper part and only 1 in the lower part. However it is worth noting that this description of stimuli could be questionable. In fact stimulus a1 could be as well described as presenting 3 elements in the upper part, 1 in the middle and 1 in the bottom part, whereas stimulus b1 could be described as presenting 2 elements in the upper part, 2 in the middle and 1 in the lower part.

Moreover, a further Experiment reported in the same paper (Turati, Valenza, Leo and Simion, 2005, Experiment 3) demonstrated that in 3-month-old babies the up-down bias does not seem to play a crucial role in determining the preference for faces. In fact, at this age a photographic image of a face (Figure 14a) is preferred over another top-heavy configuration (a scrambled configuration of face traits obtained manipulating the same photographic image, Figure 14b), in contrast to what previously demonstrated for newborn babies (Turati, Simion, Milani and Umiltà, 2002, Experiment 2; Macchi Cassia, Turati and Simion, 2004, Experiment 3). It is also interesting to note that the upper half of both the face stimulus and the non-face one are looked for longer than chance level. However, the upper half of the face-like stimulus is looked longer than the upper half of the non-face one. It is important to note that the preference for the face-like configuration observed in the present experiment could be easily explained as a preference for a symmetrical stimulus with respect to an asymmetrical one (see above).



a b

Figure 14
An example of the pairs of stimuli employed by Turati, Valenza, Leo and Simion (2005) in Experiment 3. The stimuli represent a face (a) and a scrambled version of the same stimulus, where the face traits have been arranged to represent a non-face-like top-heavy configuration (b).

It is interesting to compare with each other the results obtained in the three experiments conducted by Turati, Valenza, Leo and Simion (2005). From this comparison it emerges that the upper half of a natural face stimulus (Figure 14a), is looked longer than the upper half of the geometric non-face like top-heavy stimuli presented in Experiment 2 (Figure 13, a1, b1). Moreover, as we already mentioned, Experiment 1 provided evidence that the upper half of the face is looked longer than the lower half of the upside down face (that contains the same face traits, in the same relative positions, but presented upside down with respect to the face outline). On the other hand, Experiment 3 demonstrated that the upper half of the natural face is looked longer also with respect to the upper half of the scrambled top-heavy non-face stimulus (Figure 14b): in this stimulus the eyes are located in the upper half, but they are not embedded in a face-like configuration.

It seems thus that eyes are the most effective part of the stimulus in attracting attention at 3 months of age, but only when they are located in the upper half of the face outline and within a face-like configuration.

Thus, at 3 months of age, infants show a preference for looking at faces with respect to other stimuli, but the underlying mechanisms of this preference seem to be different with respect to those observed in newborns. The authors of this study (Turati, Valenza, Leo and Simion, 2005) interpret this change as due to the increased amount of experience with human faces that 3-month-old infants have with respect to newborn babies. However, it is impossible to exclude that maturational effects could also have a role in the differences observed between newborns' and 3-month olds.

A much more controversial point is that regarding the mechanisms determining the pattern of results obtained. In fact, the differences observed between newborns and 3-month-old infants could be interpreted as supporting the two-mechanisms model proposed by Morton and Johnson (1991), in that this model claims that a qualitative change in the mechanism that processes faces occurs during the first months of life. In fact, according to the CONSPEC-CONLERN model (Morton and Johnson, 1991), infants' behaviour would change around the second month of age, as a consequence of a shift in the mechanism in charge of controlling behaviour. Newborns' behaviour would be mainly controlled by CONSPEC, whereas after two months of age CONLERN would be the most influential mechanism. This would be due to the maturation of areas in the cerebral cortex that would be the neural basis of the CONLERN mechanism and which would inhibit the subcortical areas supposed to be the neural basis of CONSPEC. Nevertheless, Turati and her colleagues (2005) claim that their results should not be interpreted as in support of the two-mechanisms theory proposed by Morton and Johnson (1991). An alternative interpretation is on the contrary proposed for this pattern of results, emphasizing developmental continuity in the emergence of the face processing system during infancy, as opposed to the idea of a marked discontinuity in mechanisms that underlie face processing at birth and in later infancy (Nelson, 2001). This interpretation would be in line with a computational model (Bednar and Miikkulainen, 2003), which hypothesises the gradual and progressive emergence of a single system of increasing complexity, rather than the presence of two independent mechanisms that would be active in sequence. Turati and her colleagues (2005), in fact, suggest that part of the non-specific mechanisms determining the up-down bias would slowly become specialized for processing faces, due to the effect of repeated visual experience with such category of stimuli.

A source of potentially problematic evidence for the perceptual narrowing hypothesis[28] (which lays at the basis of the research on the role of non-specific biases in face perception) has been obtained in a work conducted by Macchi Cassia, Kuefner, Westerlund and Nelson (2006a) and related to that of Turati, Valenza, Leo and Simion (2005). This study tested a similar issue as that addressed by Turati and others (2005), but did so analysing Event Related Potentials (ERP) of 3-month-olds as well as their looking time in response to stimuli similar to those employed by Macchi Cassia, Turati and Simion (2004) and by Turati, Valenza, Leo and Simion (2005). This study (Macchi Cassia Kuefner, Westerlund and Nelson, 2006a) investigated whether, after 3 months of life, perceptual (and neural) narrowing for faces had taken place, leading to differential behavioural and neural responses to faces with respect to other non-face-like top-heavy stimuli (in line with the behavioural evidence obtained by Turati and others (2005) indicating that at this age infants' responses had become increasingly specific to human faces). Behavioural evidence obtained by Macchi Cassia and colleagues (2006a) confirmed the results obtained by

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[28] For a description of the perceptual narrowing hypothesis see paragraph "Broader theoretical approaches underlying this debate".

Turati and others (2005), showing that 3 months after birth top-heaviness can not explain any more the face preferences displayed by infants. In fact, infants looked at an upright face more than chance level both when it was compared with a bottom-heavy inverted face (Experiment 1, see Figure 15, a1-a2) and when it was compared with a top-heavy scrambled face (Experiment 3, see Figure 15, c1-c2). On the other hand, no preference was observed between a top-heavy and a bottom-heavy scrambled face (Experiment 2, see Figure 15, b1-b2). A possible interpretation of this last result, based on the reasoning put forward by Turati and others (2005), would be that the two stimuli employed by Macchi Cassia, Kuefner, Westerlund and Nelson, (2006a) in Experiment 2 do not present a sufficient level of up-down asymmetry. This result further confirms that the up-down bias, if still present at 3 months of age, is much weaker than it was at birth.

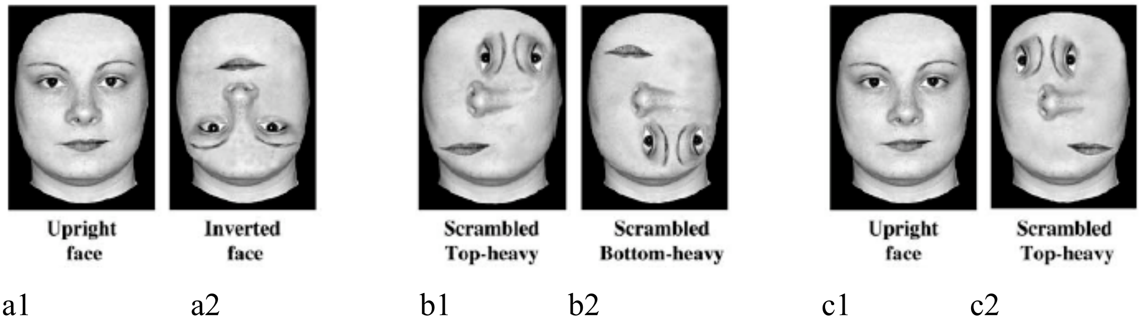

Figure 15
Stimuli employed by Macchi Cassia, Kuefner, Westerlund and Nelson (2006a). Stimuli represent an upright face (a1, c1), an upside down face where the face traits have been rotated of 180° within the face outline to represent a non-face-like bottom-heavy configuration (a2), a scrambled face whose inner features are arranged to form a top-heavy non-face stimulus (b1, c2) and a scrambled face whose inner features are arranged to form a bottom-heavy non-face stimulus (b2).

On the contrary, the ERP results obtained by Macchi Cassia Kuefner, Westerlund and Nelson (2006a) showed no evidence of the expected differentiation between faces and other top-heavy stimuli in the main components that are thought to reflect face processing in infants (the N290 and the P400, de Haan, Pascalis and Johnson, 2002; Halit, de Haan and Johnson, 2003)[29]. This is in contrast with the evidence proving that at 3 months of age the N290 and the P400 would discriminate between faces and visually matched noise stimuli (Halit, Csibra, Volein and Johnson, 2004) and between human and monkey faces (Halit, de Haan and Johnson, 2003), suggesting that at this age some amount of perceptual narrowing should have taken place and should be reflected in these two ERP components. Nevertheless, such a differential response was found in a later component, the N700, which may be related to stimulus offset and attentional disengagement (attentional disengagement would be easier from a face than from top-heavy scrambled faces, due to the novelty of this last stimulus). Macchi Cassia Kuefner, Westerlund and Nelson (2006a) interpret this result suggesting that a perceptual narrowing process has actually taken place during the first 3 months of life, leading to a behavioural response which is specific for the natural geometry of a human face (*facedness*). However, the specificity of this response would be due to attentional, rather than to perceptual mechanisms.

The role of the up-down asymmetry in modulating ERP in response to faces has been investigated also in adult subjects (Macchi Cassia, Kuefner, Westerlund and Nelson, 2006b). In this study ERP were recorded while adults made an orientation judgement on canonical faces and on distorted faces in which either the top-heaviness, or the vertical symmetry or both had been disrupted. Top-heaviness and vertical symmetry were chosen because considered fundamental defining properties of faces by the authors of this study. In general, results obtained seemed to indicate that the latency of visual ERP components related to face processing (such as the N170, but also the

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[29] The N290 and P400 are considered precursors in infants of the adult N170 component. The N170 is a negative component occurring between 140 and 200 ms over occipitotemporal regions (Itier and Taylor, 2004a, b; Rossion, Gauthier, Tarr, Despland, Bruyer, Linotte and Crommelink, 2000; Bentin, Allison, Puce, Perez and McCarthy, 1996; Botzel, Schulze and Stodieck, 1995). The N170 is thought to reflect face processing quite specifically and selectively (the N170 is supposed to reflect the configural encoding that allows for the detection of faces, Eimer, 2000a, b). As regards the infant components, it has to be noted that the literature is controversial with regard to the role of the P400. In fact there is some evidence that the response properties of the P400 can markedly differ from those of the N170 (e.g. Halit, Csibra, Volein and Johnson, 2004). It has thus been hypothesised that the P400 could be the infant precursor of later components that in adult occur after the N170 and that reflect emotion or familiarity judgments instead of face detection (Eimer, 2000a, b)

P1 and the VVP[30]) are modified linearly (in an additive fashion) in response to the combined violation of the two structural proprieties that define faces, i.e. vertical symmetry and top-heaviness. Violation of top-heaviness had however a more detrimental effect than violation of top-heaviness, within this linear additive pattern. This in turn would mean that both those properties play a role in face detection and that ERP face-sensitive responses are not driven by the unique face geometry (*facedness*). However, results not consistent with this hypothesis (i.e. that top-heaviness and vertical symmetry affect processing in an additive fashion) are also reported in the same study (Macchi Cassia, Kuefner, Westerlund and Nelson, 2006b). Exceptions to the expected linear increase-additive pattern were found for the amplitude of both of the N170 and of the VPP (influenced only by the violation of the vertical symmetry and not sensitive to top-heaviness). An analogous finding emerged also for the behavioural results (a drop in performance was observed when vertical-symmetry was violated). The authors interpret their results inferring that, whereas the timing of stimuli processing seems to be affected by both visual properties in a linearly additive fashion (with a predominant role of top-heaviness), the amount of processing required could be influenced only by the disruption of vertical symmetry. Thus, it seems that in adults top-heaviness is not the most influential property in governing face processing, in agreement with behavioural data from 3-month-olds (Turati, Valenza, Leo and Simion, 2005; Macchi Cassia, Kuefner, Westerlund and Nelson, 2006a[31]).

Research investigating the role of the up-down bias in newborns' face preferences has been commented by Johnson (2005) in a review paper. This

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[30] The P1 component (a positive component generated by the striate and extrastriate cortex at about 100-120 ms) is also considered to reflect face processing, in fact it is larger for faces than to other object categories. In particular, the P1 could reflect a holistic-processing state devoted to the perception of first-order properties that define faces (Itier and Taylor, 2002; 2004a; b; Taylor, 2002; Gonzales, Clark, Fan, Luck and Hillyard, 1994). The VPP is a positive potential occurring over centrofrontal sites simultaneously to the N170. The VPP can be larger and/or faster to faces than to other objects (Botzel, Schulze and Stodieck, 1995; Jeffreys, 1996; Rossion, Delvenne, Debatisse, Goffaux, Bruyer, Crommelink and Guèrit, 1996).

[31] However, ERP data of 3-month-olds (Macchi Cassia, Kuefner, Westerlund and Nelson, 2006a) markedly differed from adult ERP data (Macchi Cassia, Kuefner, Westerlund and Nelson, 2006b), in that infants' evoked related potentials did not differentiated between two top-heavy stimuli differing in their symmetry.

author suggests that: "*Although such preferences* [face preferences] *are sometimes said to be due to several 'domain general' biases (Turati et al., 2002), such as a putative upper visual field bias, experiments indicate that there is a crucial interdependency between the borders of the stimulus and the elements within it (Turati et al., 2002), signifying that there is some complexity to the bias. Experiments that independently manipulate upper visual field elements and bounded areas, and experiments that measure eye movements sufficiently to control presentation in the upper or lower visual field, have not yet been published "* (Johnson, 2005).

The role of such an interdependency between stimulus outline and disposition of inner elements has been recently investigated in relation to another low-level perceptual property (named 'congruency') that would generate domain general attentional biases, which in turn could be in part responsible for newborns' face preferences (Macchi Cassia, Valenza, Simion and Leo, 2008). Congruency is defined as a structural-configural property that characterises faces as well as other objects: "*Congruency can be defined, in any given pattern, by the presence of a congruent or corresponding relationship between the shape and the orientation of the bounded area delimiting the pattern and the spatial disposition of the included features*" (Macchi Cassia, Valenza, Simion and Leo, 2008). Faces, according to Macchi Cassia, Valenza, Simion and Leo (2008), do posses congruency, because the face outline appears wider in its upper than in its lower part. Thus, faces display a greater number of high contrast features (two eyes and two eyebrows) in their wider part and a smaller number of features (i.e. the mouth) in their narrower part.

See Figure 16 for the stimuli employed by Macchi Cassia and her colleagues in order to investigate the role of congruency in face preferences of newborn babies.

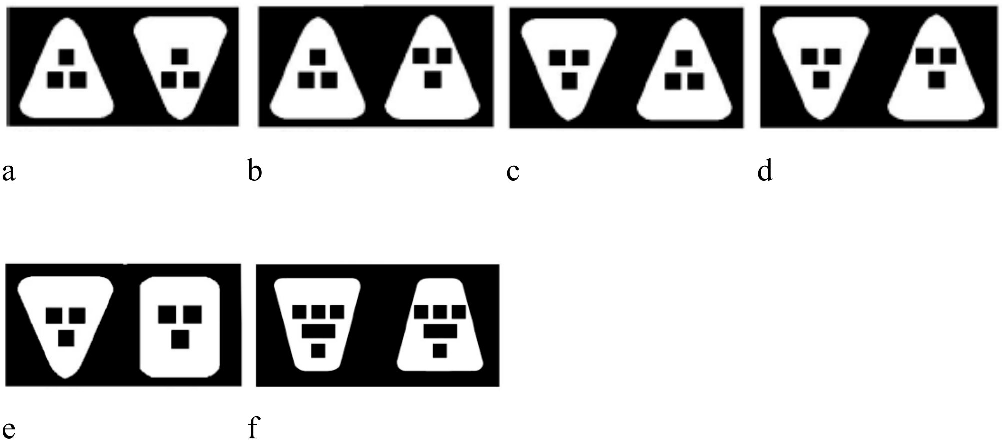


Figure 16

Stimuli employed by Macchi Cassia, Valenza, Simion and Leo (2008): a) stimuli employed in Experiment 1 representing respectively a non-face-like congruent and a non-face-like incongruent configuration; b) stimuli employed in Experiment 2 representing respectively a non-face-like congruent configuration and a face-like incongruent one; c) stimuli employed in Experiment 3, group 1, representing respectively a face-like and a non-face-like congruent configuration; d) stimuli employed in Experiment 3, group 2, representing respectively a congruent and an incongruent face-like configuration; e) stimuli employed in Experiment 4 representing respectively a face-like stimulus which is also congruent and another face like stimulus which is of neutral congruence; f) stimuli employed in Experiment 5, representing two top-heavy non-face-like stimuli, respectively a congruent and an incongruent one.

In their work, Macchi Cassia and others (2008) demonstrated that newborns prefer congruent to incongruent non-face-like displays, and also that they prefer congruent to incongruent face-like configurations (Experiments 1 and 3, group 2, Figure 16a and 16d, respectively). As expected, when both stimuli are congruent, face like displays are still preferred (Experiment 3, group 1, Figure 16c). It is necessary to note, however, that in this latter case the face-like stimulus was a top-heavy configuration and the non-face-like one was bottom heavy. As a consequence, preferences showed by newborns in group 1 (Experiment 3) could be determined by top-heaviness as well as facedness. On the contrary, no preference was observed between an incongruent face-like configuration and a congruent non-face-like one (Experiment 2, Figure 16b). Moreover, when two face like stimuli are compared, a congruent stimulus is preferred over a stimulus in which congruence is neutral (i.e. a stimulus which is neither congruent nor incongruent) (Experiment 4, Figure 16e). Finally, when two top-heavy non-face-like displays are compared, a congruent configuration is preferred over an incongruent one (Experiment 5, Figure 16f). According to the authors: "*Experiments 1 and 2 demonstrated that when embedded in nonfacelike stimuli, congruency induces a preference of the same strength as that induced by facedness. Experiments 3 and 4 demonstrated that the attentional biases toward facedness and congruency produce a cumulative effect on newborns' visual preferences according to an additive model. These findings were extended by those of Experiment 5, showing that the additive model holds true when congruency is added to top-heaviness in nonfacelike stimuli displaying more elements in the upper portion*" (Macchi Cassia, Valenza, Simion and Leo, 2008).

Observing Figure 16 it should be noted that the face-like stimuli employed by Macchi Cassia and her colleagues (2008) present inner face features very close to each other, with respect to both the natural arrangement of face features and stimuli usually employed in the literature (see Morton and Johnson, 1991; Johnson, 2005, for some examples of standard stimuli). Thus, the actual resemblance of those stimuli to a face could appear questionable, even if their inner features are disposed according to the correct triangular configuration. Similar issues have been encountered also for the face-like stimuli employed by Turati, Simion, Milani and Umiltà, (2002) in their seminal paper on the role of top-heaviness. It seems, thus, that research aiming at decomposing *facedness* in its' constituent low-level perceptual properties could be at risk of loosing *facedness* itself in the process. It is, in fact, reductive to label as "face-like" whichever stimulus that presents a triangular arrangement of inner features, regardless of its actual resemblance with a face. This point should be of great concern especially for studies aiming at investigating the role of simple perceptual properties in face preferences: in this kind of study, in fact, it should be never forgotten that *facedness* is determined by a number of simpler properties, among which the triangularity of inner features is only one and should not be considered as sufficient to label a stimulus as "face-like". Future studies may clarify this issue by employing, in experiments investigating the role of congruency in newborns' face preferences, more naturalistic stimuli, obtained from photographic images of real faces.

Moreover, by admission of the authors themselves, the data reported by Macchi Cassia and her colleagues (2008) do not allow to understand whether newborns' preference for faces and for congruent configurations are mediate by the same mechanism or by two independent mechanisms (a CONSPEC-like face detector and a non-specific preference for congruence). However, Macchi Cassia and her colleagues maintain that the first explanation would be more parsimonious and would allow for a more satisfying explanation of results obtained in Experiment 2, where a top-heavy incongruent face stimulus was confronted with a bottom-heavy non-face-like congruent one (see Figure 16b). If three independent mechanisms would be responsible for preference for top-heaviness, congruence and *facedness*, a preference would be expected for the face stimulus presenting two of the above mentioned properties (no preference was instead observed). However, this reasoning does not apply to the argumentation of the independence of the mechanisms responsible for the detection of congruence and facedness *per se*, unless the assumption that also top-heaviness has to be detected by an independent mechanism is added.

Finally, another issue is open as regards to the specific or non-specific nature of the attentional responses evoked by top-heaviness and congruency. Two interpretations are possible on this regard. The first interpretation would be that these general attentional biases are a parsimonious way by which the human visual system solves the problem of detecting faces. The second possible interpretation would be that because congruency and top-heaviness are two defining property of facedness, a CONSPEC-like face detection template matches better with congruent as well as top-heavy stimuli.

It is interesting to note that some recent publications (e.g. Macchi Cassia, Valenza, Simion and Leo, 2008; Farroni, Johnson, Menon, Zulian, Faraguna and Csibra, 2005) seem to indicate a convergence of ideas between the two main strains of research present in this field (one supporting the CONSPEC-CONLERN model and the other supporting the presence of general attentional biases triggered by low-level perceptual properties). In fact, in both the above mentioned papers, authors tend to stress the fact that non-specific attentional biases (such as the up-down bias) can be considered as domain relevant, in that they allow newborns to successfully select faces among other objects that can be often encountered in the natural environment without originating too many false alarms (i.e. erroneous positive responses to non-face-objects). From the phylogenetic/adaptive point of view, in fact, there could be little difference between a specific predisposition to look at stimuli that present the precise structure of a face and a collection of general biases for perceptual properties that characterise faces and whose cumulative effect would be indistinguishable from that of a face-specific mechanisms. Of course, the theoretical debates discussed before render the investigation of the detailed mechanism underlying face preferences still relevant to future studies.

At this point, a comparison with animal data on non-specific biases in face preferences seems appropriate. Such a comparison is possible as regards the work of Kuwahata, Adachi, Fujit, Tomonaga and Matsuzawa (2004). The study by Kuwahata and colleagues (2004) is, at the best of our knowledge, the only one to have (indirectly) investigated the role of non-specific biases, such as the up-down bias, in spontaneous face preferences in animal species (infant macaque monkeys, in this case). In fact, one of the pairs of stimuli employed (pair B) consisted in a face-like and a non-face-like display balanced in terms of the up-down bias (i.e. both stimuli were top-heavy configurations presenting two elements in the upper part and only one in the lower part, see Figure 4). Moreover, both stimuli where symmetrical along the vertical axis. The face-like stimulus was nevertheless preferred over the non-face-like one. Thus, the putative role of the up-down bias in determining spontaneous face preferences, could be limited to the human species. Unfortunately, however, in this work (Kuwahata, Adachi, Fujit, Tomonaga and Matsuzawa, 2004), visual experience with conspecifics' (and, possibly, also humans') faces was not controlled prior to the moment of the test (test started during the 1st month of life, but some animals were tested after 2 months of life), thus paralleling the lack of control on visual experience typical of studies with human infants. Moreover, the wide age-range of monkeys at the time of test adds further variability in the amount of previous visual experience available to subjects, with respect to what is usually the case in human infant studies.

Carefully controlled studies with precocial animal species (such as the domestic chick), easy to test shortly after birth/hatching, and thus allowing a good level of control over previous visual experience with relevant stimuli, seems clearly needed to clarify the issues described in this session. We thus decided to employ visually naïve domestic chicks in order to investigate the presence of spontaneous preferences for schematic face-like stimuli and the role of the up-down bias in such preferences.

## Introduction to Experiment 5: Role of spatial frequencies composing stimuli in face preferences

As already mentioned above (se paragraph "The structural and the sensory hypothesis"), one of the most influential accounts of human infants' visual preferences is that known as sensory hypothesis, maintaining that visual preferences at birth would be determined merely by the visibility of stimuli. According to the sensory hypothesis infants prefer to look at stimuli that maximise the amount of energy conveyed to the infant's sensory system, due to the good match between stimuli low-level psychophysical properties and the features of infants' visual system. One of the most successful versions of the sensory hypothesis was that based on the Linear System Model (LSM, Banks and Ginsburg, 1985; Banks and Salapatek, 1981; Gayl, Roberts and Werner, 1983; Kleiner, 1993; 1987; 1990; Kleiner and Banks, 1987; Slater, Earle, Morison and Rose, 1985). This model is relevant to the present work because it considers a physical property, namely spatial frequencies (SF) composing stimuli, the crucial factor in determining human infants' preferences for visual stimuli, including faces.

Spatial frequency is a characteristic of any structure that is periodic across space. In fact, it measures how often the structure repeats per unit of distance. In general, low spatial frequencies (LSF) are thought to convey coarse visual information (large scale variations of luminance ranges), whereas high spatial frequencies (HSF) convey fine visual information (tighter gradients of luminance variations).

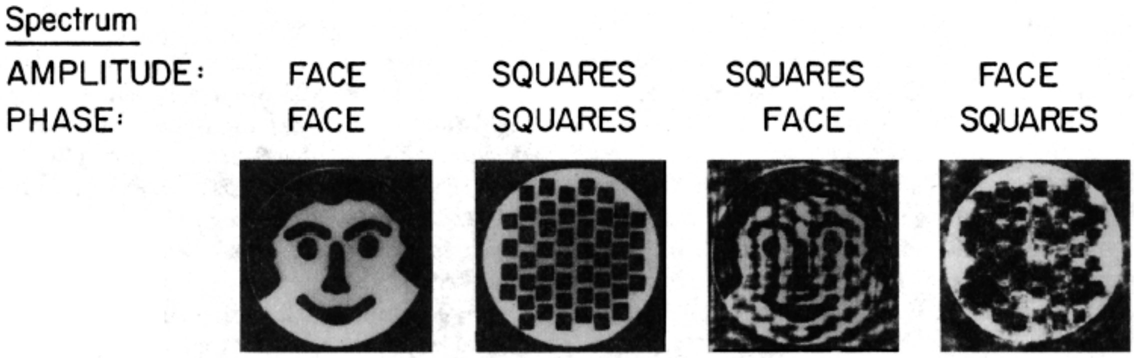
The idea that stands at the basis of the LSM is that newborns prefer to look at what they see better. According to this theory, two kind of factors would be relevant for visual preferences.

The first factor to be taken into account is the subject's Contrast Sensitivity Function (CSF), a function which indicates the inverse of the contrast that is necessary for the subject to detect sine waves of different spatial frequencies. In newborns, vision is limited and as a consequence only low spatial frequencies may be processed (Atkinson, Braddick and Moar, 1977; Banks and Ginsburg, 1985). What newborns see better is large stimuli of high contrast, having a preponderance of low spatial frequencies. Actually, human newbons' CSF has not been systematically measured. Nevertheless, in the literature there is evidence that in newborns the visual acuity (the maximum spatial frequency that can be seen) is of about 1 cycle/degree (c/d) and that the best acuity is observed for frequencies between 0.1 and 0.2 c/d (which are thus the spatial frequencies best seen by the newborn, that is the spatial frequencies corresponding to a maximum value for the CSF) (Slater and Sykes, 1977). Moreover, Acerra, Burnod and de Schonen (2002), recently simulated a possible CSF of newborn babies, based on the fitting of a neural network model with behavioural data on infants' visual preferences (see below for a description of the model).

The other crucial factor to be considered in order to predict newborns' visual preferences according to the LSM, would be the physical properties that describe stimuli and that can interact with newborns' CSF. As it will be explained below, spatial frequencies have a crucial role among these properties. This approach is based on the mathematical analysis of physical properties of visual stimuli on the basis of a procedure known as linear system analysis that computes the Fourier transform of a visual pattern. This allows to decompose stimuli in sine waves of different spatial frequencies. Any two-dimensional achromatic pattern can then be described on the basis of properties of its constituent sine wave gratings, namely their spatial frequencies, amplitude (contrast), orientation, and phase. Thus, for any given pattern, two functions can be derived: the Amplitude Spectrum (AS), determined by the amplitude and orientation of the component spatial frequencies, and the Phase Spectrum (PS), which is on the contrary determined by phase and orientation of the components. The amplitude spectrum is responsible for the amount of energy conveyed by the stimulus. The phase spectrum, on the contrary, conveys stimuli structure. For example, only stimuli presenting the PS of faces look face-like to human adults, whereas the mere presence of the AS of faces is not sufficient for the recognition of stimuli as faces (Piotrowski and Cambpell, 1982).

According to the LSM, infants' visual preferences for a given pattern can be explained by the AS of the pattern filtered by the CSF of the appropriate age group (in newborns this is accomplished by removing SF grater than 2 c/d). Infants prefer patterns whose filtered amplitudes are grater, regardless of their structure. In this account, faces should not be different from other stimuli: they are preferred simply because they happen to have an AS that better matches the CSF of a newborn baby.

The LSM has been demonstrated capable of predicting infants' preferences for a wide range of stimuli (e.g. Banks and Ginsburg, 1985; Banks and Salapateck, 1981; Gayl, Roberts, and Werner,1983; Slater, Earle, Morison and Rose, 1985). As regards face preferences, a crucial study aimed at testing the LSM's predictions is the one by Kleiner (1987). The two basic stimuli employed by this author were a schematic face (Figure 17a) and a lattice pattern (also called squares pattern) (Figure 17b). These original stimuli were analyzed with a Fourier transform in order to obtain the component AS and PS. These spectra were then recombined to create two crossed stimuli, one with the AS of the face and the PS of the lattice (Af/Pl, Figure 17d) and the other with the AS of the lattice and the PS of the face (Al/Pf, Figure 17c).



a b c d

Figure 17

This image (taken from Kleiner and Banks, 1987), illustrates stimuli employed by Kleiner (1987) and Kleiner and Banks (1987) and their properties. Stimulus a) represents a schematic drawing of a face (it thus has both the AS and the PS of a face, Af/Pf); stimulus b) represents a lattice pattern, or square pattern (it thus has both the AS and the PS of a lattice, Al/Pl); stimulus c) was obtained combining the AS of the lattice pattern and the PS of the face (in fact the face like structure is still recognizable to adults, Al/Pf); finally stimulus d) was obtained combining the AS of the face pattern and the PS of the lattice one (in fact this pattern is not recognizable as a face any more, Af/Pl).

According to the LSM, newborns' preferences would be determined completely by AS, whereas the PS would not have any influence. Thus, stimuli that present the AS of the face should always be preferred over stimuli that presented the AS of the lattice pattern, regardless of the PS (i.e. of stimuli structure). The underlying assumption of this prediction is that the AS of the face is optimal for the newborn visual system.

Most of the results obtained in this study are in agreement with the predictions of the LSM. As predicted by both the LSM and the CONSPEC-CONLERN model, newborns' preferred the face (Af/Pf, Figure 17a) over the lattice pattern (Al/Pl, Figure 17b). When newborns were presented with the comparison between the lattice stimulus (Al/Pl, Figure 17b) and the crossed stimulus with the AS of the lattice and PS of the face (Al/Pf, Figure 17c), they showed no preference. In the comparison between the stimulus with the AS of the face and the PS of the lattice (Af/Pl Figure 17d) and the stimulus with the AS of the lattice and PS of the face (Al/Pf, Figure 17c), the former was preferred (this later result has been subsequently confermed by Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens and Kleiner-Gathercoal, 1999, using an alternative test procedure). These results indicated that, in the comparisons considered up to the present moment, the phase had no influence on newborns' preferences.

However, some researchers (Morton, Johnson, and Maurer 1990; Morton and Johnson, 1991) have pointed out that at least part of the data reported by Kleiner (1987) for newborn babies are against the predictions of the LSM. According to the LSM phase information should not influence newborns' preferences, and thus the crossed stimulus presenting the AS of the face and the PS of the lattice stimulus (Af/Pl, Figure 17d) should be equally preferable to the face stimulus having both AS and PS of a face (Af/Pf, Figure 17a). On the contrary this later stimulus results preferred, even if differing from the first only in its PS. Morton and Johnson (1991) considered this result obtained by Kleiner (1987) as in favour of the presence of a mechanism that: "*…contains structural information, that is, some specification of the features of a face together with their relative location in space. The reader should note at this point that we are not rejecting the notion of the linear systems model nor would we expect facelike stimuli to be preferred over all other stimuli*" (Morton and

Johnson, 1991). In fact, the same authors obtained themselves evidence that a checkerboard pattern, designed to have optimal visibility for newborns was preferentially looked at with respect to a schematic face (see Morton and Johnson, 1991 for a review).

As a consequence of this objection, Kleiner (1990) proposed the LSM model in a revised version, hypothesizing a sequential (hierarchical), two-stage model. According to this new version, the AS would still be the primary determinant of newborns' preferences. However, if two stimuli would present an identical AS, then the PS would make the difference. In fact, stimuli would be first compared for their amplitude and then, only if they do not differ on this property, their structure would be also taken into account. The preference for the structure of a face is explained in this context as a learning effect.

It is interesting to note that by two months of age, infants' preferences were on the contrary completely driven by the PS of the stimuli (Kleiner and Banks, 1987). At this later age, in fact, infants showed a preference for all the stimuli presenting the PS of a face (Af/Pf, Figure 17a, and Al/Pf, Figure 17c) over any other stimulus presenting the PS of the lattice (Al/Pl, Figure 17b, and Af/Pl, Figure 17d) (again, this result was confirmed by Mondloch, Lewis, Budreau, Maurer, Dannemiller, Stephens and Kleiner-Gathercoal, 1999, in both 6- and 12-week-old babies). Between the two patterns presenting the phase of a face, the pattern presenting also the amplitude of a face was preferred (Af/Pf, Figure 17a, was preferred over Al/Pf, Figure 17c), signaling that AS still had a role in infants preferences. Finally, no preference was observed between the two patterns that had the PS of a lattice (Al/Pl, Figure 17b, and Af/Pl, Figure 17d). According to Kleiner and Banks (1987), their results could be explained both by a shift in the mechanism responsible for face preferences and by an increased interest in faces displayed by 2-month-olds as a consequence of their increased experience with that kind of stimuli (the first interpretation was favoured by the authors). Thus, results obtained by Kleiner and Banks (1987) in newborns and in 2-month-olds are in agreement with the model put forward by Morton and Johnson (1991), in that they may indicate a qualitative change in mechanisms responsible for face preferences between birth and the second month of age.

A crucial study that confronted the CONSPEC-CONLERN model with the LSM in its original and revised version is that conducted by Valenza, Simion, Macchi Cassia and Umiltà (1996). The first experiment conducted in this study (Experiment 1), confirmed the presence of a preference for schematic face-like stimuli with respect to similar stimuli having the inner features rotated of 180° (i.e. presented upside down) within a normally oriented face outline (Figure 18, a and b). The two stimuli employed by Valenza and her collaborators (1996) in the first experiment are reported to have nearly identical amplitude spectrum. This experiment demonstrated the presence of a preference based on the structural configuration of the stimulus, and namely on the face-like arrangement of inner features, using two different testing techniques (a traditional preferential looking technique and a different procedure involving unilateral stimulus presentation). Due to the fact that stimuli differed mainly in their structure (PS) the results obtained in Experiment 1 disconfirmed the original version of the LSM, according to which PS should have no role in infants' preferences (but were still compatible with the revised version of the same model). The second experiment conducted by Valenza, Simion, Macchi Cassia and Umiltà (1996) was aimed at confirming that newborns' preferences can be determined by AS. In fact newborns were presented with a pair of non-face-like stimuli. For one stimulus, inner features were plain black blobs, whereas for the other stimulus inner features were striped blobs of the spatial frequency optimal according to the CFS estimated for newborns (Figure 18, c and d). The prediction originated by the LSM was confirmed, in that newborns looked more to the stimulus with stripped blobs than to the stimulus with plain black blobs. Note however that this result is not in contrast with the CONSPEC-CONLERN model, because no face-like stimulus was present. Finally, in a third experiment, newborns were presented with a face–like stimulus with black blobs and a non-face-like stimulus with stripped blobs (that was preferred in Experiment 2) (Figure 18, e and f). The face-like stimulus resulted preferred even if it was compared to a stimulus of higher physical salience for the visual system of the newborn.

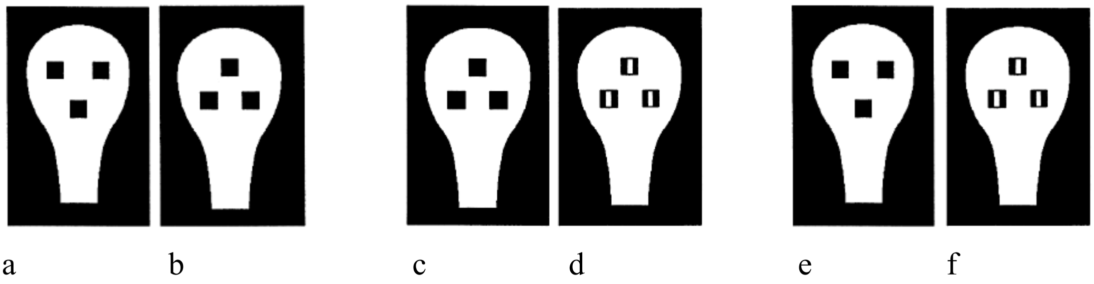


Figure 18
Stimuli employed by Valenza, Simion, Macchi Cassia and Umiltà (1996). The first pair of stimuli (a and b) were employed in Experiment 1. They represent a schematic face-like stimulus (a) and a non face-like one obtained rotating the inner features of the face stimulus of 180° within the face outline (b). The second pair of stimuli (c and d) was employed in Experiment 2. They represent a non-face-like stimulus of low physical salience whose inner features are constituted of plain black blobs (c) and a non-face-like configuration of higher physical salience whose inner features are constituted of stripped blobs of the spatial frequency most visible to newborns (d). The third pair of stimuli, employed in Experiment 3, confronted the two configurations preferred by newborns: the face-like configuration of low-physical salience preferred in Experiment 1 (e) and the non-face-like stimulus of higher physical salience according to component spatial frequencies preferred in Experiment 2 (f).

Results obtained in this study thus were strongly in favour of the CONSPEC-CONLERN model (Morton and Johnson, 1991) when confronted with both the original and the revised version of the LSM model (Kleiner, 1987; 1990).
However, some aspects of the data obtained by Valenza and her colleagues (1996) do not fit well with the CONSPEC-CONLERN model, according to which the mechanism responsible for face preferences at birth would be subcortical (Morton and Johnson, 1991; Johnson, 2005). First of all, most of significant effects obtained by Valenza and colleagues (1996) were limited to dependent variables associated with fixation times and not with dependent variables associated with gaze orienting responses. This is relevant because in developmental literature fixation time is considered an index of cortical functioning, whereas orienting responses are considered an index of sub-cortical functioning (but see Simion, Valenza, Umiltà, and Della Barba, 1998, for an alternative interpretation of these results). Moreover, a lateralization

effect also emerged in Experiment 3: the preference for the face-like stimulus was evident only when it was presented to the left. This left visual-field advantage for face preferences is suggestive of a right hemisphere specialization for face processing (see also de Schonen and Mathivet, 1989), that points toward an involvement of the cerebral cortex in the results obtained. Possibly inspired by these indexes of cortical involvement in newborns' face preferences, Acerra, Burnod and de Schonen (2002) proposed a neural network model of infants' face preferences based only on the response properties of neurons in the primary visual cortex (V1)[32]. This study is relevant for the purposes of the present work because Acerra and her colleagues have been able to simulate the very results obtained by Valenza, Simion, Macchi Cassia and Umiltà (1996) in favour of the CONSPEC-CONLERN model, by simply implementing in their model some of the basic response properties of V1 neurons and some of the constraints imposed by newborns' immature visual system (without hypothesising any explicit prewired representation of faces' structure). The first of the features that Acerra, Burnod and de Schonen (2002) implemented in their model was the selectivity of V1 neurons for spatial frequencies, whereas the second was the CSF of newborn babies (see above). This model thus reopens the controversy regarding the role of spatial frequencies in human newborns face preferences. Two basic properties may be sufficient to generate face preference at birth: tuning selectivity for spatial frequencies and limited vision.

The rationale for a model based on V1 neurons' response properties is that, unlike many other cortical areas that at birth present very small neurons with short dendrites (included areas responsible for face processing in adults, such as the Fusiform Face Area), in V1 neurons appear to have the potentiality to be at least in part functionally active during the first days of life. Moreover, neurophysiological studies in cats and monkeys have demonstrated that neurons in the striate cortex are selective to the spatial frequency of sine wave gratings (Albrecht, De Valois and Thorell, 1980; Movshon, Thompson and

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[32] Models that explain adult face processing in terms of activation of a set of spatially distributed filters selective, among other things, for spatial frequencies are reviewed in Biederman and Kalocsai (1997). It is worth noting that such models are able to account for many of the hallmarks of face processing. Moreover, the models presented by Biederman and Kalocsai (1997) assume that face processing is more dependent on the pattern of activation of frequency selective filters with respect to object processing.

Tolhurst, 1978; Schiller, Finlay and Volman, 1978; Tootel, Silverman and De Valois, 1981). As V1 neurons are assumed to be sensitive to spatial frequencies occurring in one position of the visual filed (receptive field), the model proposed by Acerra, Burnod and de Schonen (2002) differs from the LSM in that it does not assume each neuron to be sensitive to the spatial frequencies in the whole image (as computed by the Fourier Transform for the whole stimulus). In the model put forward by Acerra, Burnod and de Schonen (2002), in fact, each neuron is sensitive for one position in the image and one spatial frequency, in a way that its activity corresponds to the local amplitude of the given spatial frequency. Preference is determined by the overall activity of the network for a given stimulus (filtered by the actual spatial frequencies that a newborn is able to see). In particular, the neural network model developed by Acerra and her colleagues was able to replicate the crucial hierarchy of preferences among the stimuli (reported in Figure 18, a, b and d) that was originally obtained by Valenza, Simion, Macchi Cassia and Umiltà (1996). Stimulus 18a was preferred over 18b and 18d, whereas stimulus 18d was preferred over 18b. Relevantly, even the preference for the face-like stimulus over the two non-face-like ones is explained by the authors in terms of the spatial frequencies composing the stimuli. In fact, the position of the inner blobs within the face outline influences the regularity of the spacing between the blobs themselves and between the blobs and the outline of the face. This spacing results more regular in a face-like arrangement than in a non face-like one: in a face-like stimulus the distance between the blobs is roughly the same as blobs' dimension and as the distance between the blobs and the outline (see Figure 19 for a graphical description). This would thus account for the preferences expressed by the neural network model, which in fact is sensitive only to spatial frequencies composing stimuli. Regularity of spacing increases the amplitude of the corresponding spatial frequency.

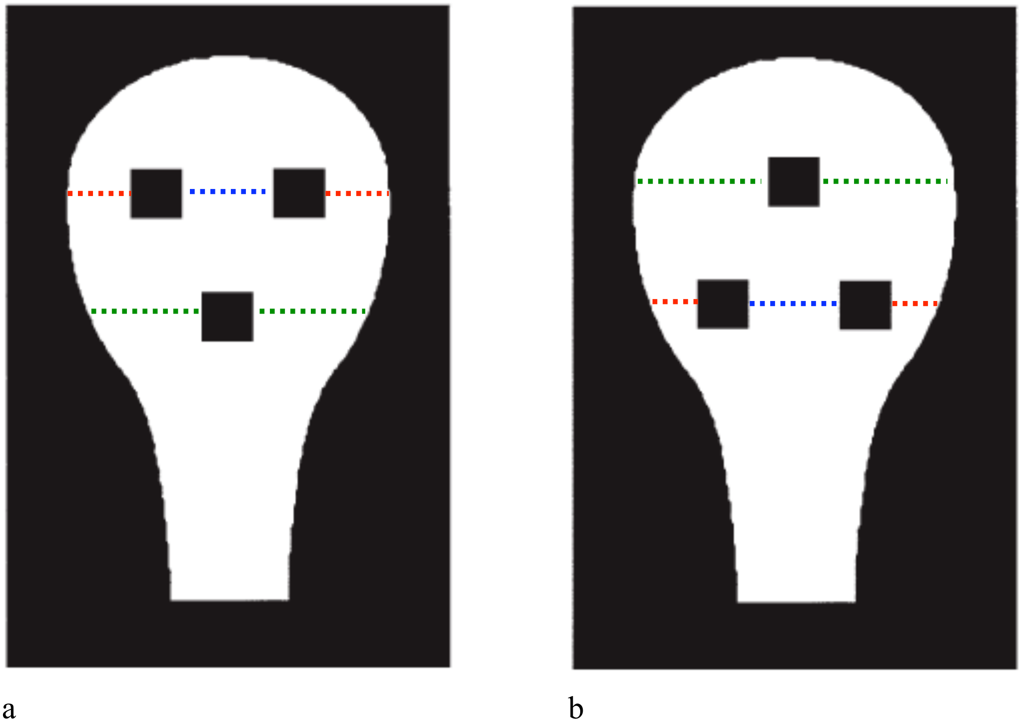

Figure 19

This figure illustrates the argumentation of Acerra, Burnod and de Schonen (2002), that the spacing between the blobs themselves and between the blobs and the outline is more regular in a face-like display. In fact, in a) the difference between the length of the red dotted lines (representing the distance between the blobs and the outline) and the length of the blue dotted line (representing the distance between the two blobs), is reduced with respect to b).

Moreover, in a), the length of the green dotted line (representing the distance between the lower blob and the outer contour) is reduced with respect to the length of the corresponding green dotted line in b). Thus, the green line's length is more similar to the length of the red and blue lines in a) than in b).

Regularity of spacing would also explain the preference expressed by the neural network model for a stimulus representing a checkerboard within a face outline (Figure 20), which elicited higher activation, in the neural model proposed by Acerra, Burnod and de Schonen (2002), with respect to all the other stimuli presented. This result is consistent with behavioural data on newborn babies, which have been also demonstrated to prefer this checkerboard stimulus to many other stimuli (see Morton and Johnson, 1991)[33].

Figure 20

Checkerboard stimulus employed by Acerra, Burnod and de Schonen (2002).

It should be noticed however that Acerra, Burnod and de Schonen (2002) consider their model structurally similar to that put forward by Morton and Johnson (1991), except for the fact that a different underlying mechanism and a different neural substrate is hypothesised for a similar function. Acerra, Burnod and de Schonen (2002) believe that "… *the cumulative and combined effects of these properties* [V1 neurons' response properties, N.d.A.] *give a 'statistical' advantage to faces with respect to other stimuli… This is somewhat in agreement with Johnson and Morton's idea (1991, p. 135) except that we believe that, contrary to Morton and Johnson (1991), these properties correspond to the activity of V1*". Moreover, Acerra and her colleagues do not exclude the possibility that a subcortical mechanism could participate to newborns' face preferences, in parallel with V1. The authors, in fact, present their model as an attempt of integrating the LSM with the CONSPEC-

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[33] Sensitivity to regular spacing, and thus the preferences described above, can be accounted for by the present model, but could not be accounted for by the LSM model. This is because the LSM considered the AS (which is position-independent, being computed on the whole image) as the crucial property. On the contrary, for the model of Acerra, Burnod and de Schonen (2002), the crucial property is the overall activation level of a population of units (V1 neurons), each one sensitive to the amplitude of the signal corresponding to a certain spatial frequency in a certain location of the image.

CONLERN model: "*In essence, this face-preference model can be seen as both a neural LSM and a computational CONSPEC. The tuning properties of V1 neurons and the limitations of an immature CSF, together lead to CONSPEC-like behaviour. This first layer simulates a neural face-preference module, which biases, like CONSPEC, the newborn visual attention towards a facelike structure, and moreover filters visual information*".

As a final note of caution, it should be remembered that results obtained by Acerra, Burnod and de Schonen (2002) were highly dependent on the exact shape of the schematic stimuli employed (see Figure 19), which determined the precise distance between the inner features and the stimulus outline (the crucial factor in determining the net responses, see above). It can reasonably be questioned whether the same results could be obtained employing different configurations (e.g. more naturalistic stimuli or even other schematic stimuli already used in the literature) (Bednar and Miikkulainen, 2003).

When considering the role of spatial frequencies in face preferences, it is also interesting to note that it has been recently demonstrated that newborns' recognition of individual faces is based on spatial frequencies below 0.5 c/d (i.e. only on low spatial frequencies, the lower ones even among the range of spatial frequencies perceived by newborns) (de Heering, Turati, Rossion, Bulf, Goffaux and Simion, 2008, Experiment 2)[34]. However, a first experiment conducted within the same study demonstrated that newborns are able to extract from a face the visual information lying from 0 to 1 c/d (de Heering, Turati, Rossion, Bulf, Goffaux and Simion, 2008, Experiment 1). Overall, results obtained in this study mean that the band of spatial frequencies available to newborns for face recognition overlaps with that available for recognition of stimuli other than faces, such as gratings. Moreover, within the frequency range visible to newborns, lower spatial frequencies are the most effective in conveying information for visual recognition of individual faces. De Heering and her colleagues (2008) trace some interesting conclusions from their data and from the fact that, plausibly, in adults LSF play a major role in high-level face processing. De Heering and others in fact argument that: "*the face recognition system may progressively stabilize its synaptic connections in*

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[34] This is not surprising if we consider that this is also the range of frequencies for which the best acuity is observed in babies (Slater and Sykes, 1977).

*relation to lower rather than higher spatial frequencies, and therefore emerge as the result of the combined effect of perceptual constraints that may be lead back to the properties of the infant's visual processing system (de Schonen and Mathivet, 1989)… non-specific constraints of the newborns' visual system (CSF) combined with peculiar visuo-perceptual characteristics of the face stimuli (LSF) force newborns to process those aspects of a face that deal with large scale variations rather than subtle variations provided by fine details. Non-specific constraints of the perceptual system interacting with certain systematic variations present in the surrounding environment may thus allow increasing neurocognitive specialization of face processes with development*" (de Heering, Turati, Rossion, Bulf, Goffaux and Simion, 2008). On this regard it is interesting to remember that human newborns show, like adults, a dominance of global properties in the processing of visual objects (note that holistic-configural processing is even more pronounced for faces that for other classes of objects). This global bias is strictly dependent on LSF (Macchi Cassia, Simion, Milani and Umiltà, 2002).

The role of low spatial frequencies in newborns' face recognition is however also in agreement with the theory, put forward by Johnson (2005), of a fast-and-rough subcortical face detection route that processes low spatial frequency information. This subcortical route would comprise the main mechanisms responsible of newborns' face processing. The subcortical route would be, however, still active even in adults (where the cerebral cortex is clearly in charge of many operations involved in face processing), to allow for the rapid detection of faces. It is worth noting that it has been hypothesized that adult face processing would be more sensitive to SF variations as compared to object categorization (Biederman and Kalocsai, 1997; Collin, Liu, Troje, McMullen and Chaudhuri, 2004). As regards human adults, in the literature evidence is there suggesting that optimal face recognition would be based on an intermediate band of spatial frequency (Näsänen, 1999; review in Costen, Parker and Craw, 1996; Morrison and Schyns, 2001; Parker and Costen, 1999[35]; but see also Liu, Collin, Rainville and Chaudhuri, 2000). More recently, it has been shown that a crucial factor for face recognition in adults seems to be the overlap in SF across face stimuli presented during encoding

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[35] For contrasting evidence see Bruce, Hanna, Dench, Haley and Burton (1992).

and for recognition (e.g. Liu, Collin, Rainville and Chaudhuri, 2000; Collin, Liu, Troje, McMullen and Chaudhuri, 2004). However, it has been hypothesized that the processing of face configurations would be mainly subtended by LSF that convey coarse information (Goffaux and Rossion, 2006; Goffaux, Hault, Michel, Vuong and Rossion, 2005; Morrisson and Schyns, 2001).

In fact, in the adult face perception, high- and low-spatial frequency information (i.e. information at fine and coarse spatial scales) is used selectively according to the task performed (Goffaux, Jemel, Jacques, Rossion and Schyns, 2003; Gosselin and Schyns, 2001; Schyns, Bonnar and Gosselin, 2002; Schyns and Oliva, 1999). Low Spatial Frequencies (LSF) preserve only the configuration of stimuli (a crucial information for face processing), whereas High Spatial Frequencies (HSF) convey information about fine details. As already mentioned above, in general a prevalence of the use of LSF has been observed for configural processing of faces: the use of line drawings (that alter the representation of coarse cues, Biederman and Ju, 1988) impairs configural face processing (Leder, 1996). Similarly, a strong face inversion effect (a hallmark of configural face processing) is observed in blurred faces in which HSF information was attenuated (Collishaw and Hole, 2000; 2002), with recognition performance of inverted blurred faces at chance level. Also the whole-part advantage and the composite-face effect (that are two other indexes revealing holistic/configural processing of faces) rely mainly on the presence of LSF information (Goffaux and Rossion, 2006). Discrimination of two faces is performed more accurately on LSF face images when stimuli differ because of their configural properties, whereas performance is higher on HSF faces if stimuli differ because of changes in local features (Goffaux, Hault, Michel, Vuong and Rossion, 2005). Another example of the differential use of HSF and LSF information according to the task performed by adults has been shown using hybrids obtained superimposing the images of two faces of different expression (e.g. one face had a neutral expressions, whereas the other face was expressing one emotion) and gender. One of the two faces was filtered leaving only HSF and the other only the LSF (Schyns and Oliva, 1999). Schyns and Oliva reported that subjects tended to rely on the HSF information when asked whether the face was expressive or neutral, but on the LSF when asked to identify the emotion expressed. Similarly, using a different technique, it was demonstrated that subjects tend to use predominantly LSF information in a gender categorization task but not in an identification task (Gosselin and Schyns, 2001; Schyns, Bonnar and Gosselin, 2002; Goffaux, Jemel, Jacques, Rossion and Schyns, 2003). As regards ERP studies some data were obtained in favour of a crucial role of LSF in adult face processing, showing that the N170 amplitude was not significantly different between normal faces and LSF faces, whereas it was reduced for HSF faces. Moreover, there was a greater N170 amplitude in a gender categorization task with respect to a familiarity recognition task. Similarly, in the gender task the N170 amplitude was greater when stimuli were LSF faces with respect HSF faces (Goffaux, Jemel, Jacques, Rossion and Schyns, 2003). The advantage of LSF information in modulating the N170 amplitude seems to be specific for faces. The characteristic larger amplitude of the N170 for faces with respect to objects is present only when stimuli are LSF images but not when they are HSF images. Moreover the N170 amplitude is larger to LSF than HSF faces, but not to LSF than LSF objects. Using LSF face images it is also possible to observe the typical delay in the latency of the N170 to inverted faces with respect to upright faces, but this effect is absent in HSF images (no such inversion effect was ever observed when stimuli were images of non-face objects, regardless of the spatial frequencies composing the images). Finally, a right hemisphere advantage was observed in the amplitude of the N170 for LSF faces, but not for HSF faces or non-face objects. Thus all the face specific effects usually observed in the N170 are preserved in LSF images and absent in HSF images (Goffaux, Gauthier and Rossion, 2003).

In consideration of the lack of certain, detailed or conclusive data on newborns' CSF and on the role of spatial frequencies in face processing in general (and in particular in newborns' visual preferences) a reasonable approach seems to be that of testing face preferences employing control stimuli that are matched in terms of their component spatial frequencies. This approach has been recently employed by some studies reported in the developmental literature. Such studies were aimed at investigating the neural correlates of face perception through the use of EEG-ERP techniques (e.g. Halit, Csibra, Volein and Johnson, 2004) and of neuroimaging techniques (e.g. Csibra, Henty, Volein, Elwell, Tucker, Meek and Johson, 2004; Blasi, Fox, Everdell, Volein, Tucker, Csibra, Gibson, Hebden, Johnson and Ellwell, 2007). The use of frequency matched control stimuli would be obviously advantageous with respect to the use of images of non-face objects or scrambled faces, in that it would allow to control the role of spatial frequencies. Moreover, it has been pointed out that the use of frequency matched control stimuli would be advantageous also with respect to the use of inverted (upside down) faces, because uncertainty remains about the regularity with which newborns of different species (e.g. humans, but also domestic chicks) view faces rotated in the vertical axis (Halit, Csibra, Volein and Johnson, 2004).

Halit, Csibra, Volein and Johnson (2004) recorded ERP from both adults and 3-month-olds while they viewed faces and matched visual noise stimuli. Noise stimuli were matched with respect to faces in terms of frequency content, colour distribution and outer contour (see Figure 21 for examples of stimuli employed by Halit and colleagues).

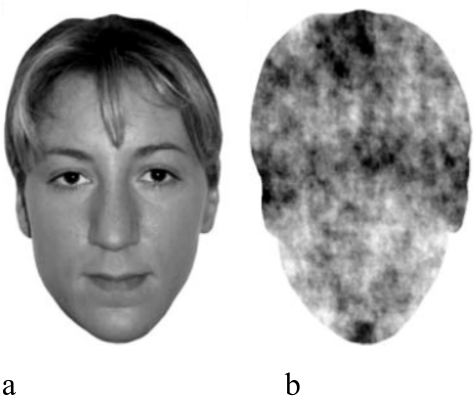

Figure 21

Examples of stimuli employed by Halit, Csibra, Volein and Johnson (2004). Stimuli were a) photographic colour images of faces and b) visual noise stimuli matched in frequency content, colour distribution and outer contour to the face stimuli. Noise stimuli were created randomizing the phase spectra of faces, whilst keeping the amplitude and colour spectra constant.

In this study by Halit, Csibra, Volein and Johnson (2004), the adult ERP component N170 and its possible infant precursor the N290[36] showed an increased amplitude to faces with respect to visually matched noise stimuli. Thus faces elicit a specific cortical response with respect to stimuli that share the same spatial frequency as early as 3 months after birth. The results obtained in this experiment are particularly interesting because they confirm the pattern of results classically described in the literature when faces are compared with other non-face-like stimuli. Thus, the work of Halit, Csibra, Volein and Johnson (2004) validates the use of frequency-matched noise stimuli in human face perception studies.

Similarly, Csibra, Henty, Volein, Ellwell, Tucker, Meek and Johnson (2004) demonstrated (using the Near Infrared Spectroscopy, NIRS, neuroimaging technique) an increase of metabolic activity in occipital regions while adults viewed a face stimulus (the colour photographic image of a woman's face) with respect to a visually matched noise stimulus. The noise stimulus was a scrambled configuration, artificially constructed by digital manipulation in order to contain the same colour distribution and the same spatial frequencies as the face stimulus (see Figure 22 for an example of stimuli employed).

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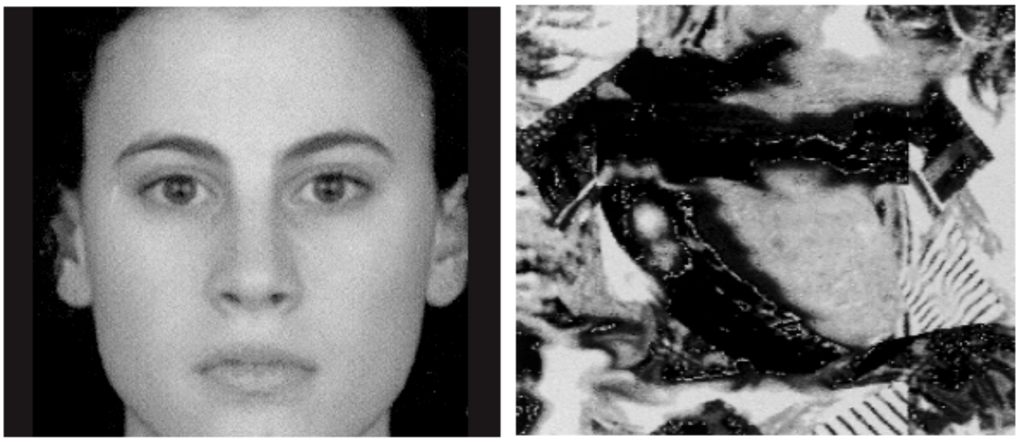
[36] The adult component N170 and the infant component N290 are thought to specifically reflect face processing (see before). Some authors have suggested that in infants also the component known as P400 could be considered an infant precursor of the adult N170. In the present study, however, the P400 component showed a response pattern which was markedly different from that of the N170: the P400 showed no amplitude effects and instead peaked earlier for noise than for face stimuli, leading the authors to conclude that the P400 can not be considered as a precursor of the N170, whose response properties are better mirrored by the N290 infant component.



a b

Figure 22

Examples of the stimuli employed by Csibra, Henty, Volein, Ellwell, Tucker, Meek and Johnson (2004). Stimulus a) is a grey scale reproduction of one of the colour photographic images of female human faces; stimulus b) is a grey scale reproduction of the noise stimulus that was digitally constructed to contain the same spatial frequencies and colour distribution as the corresponding face stimulus. Noise stimuli were created as described for those employed by Halit, Csibra, Volein and Johnson (2004), Figure 21.

Csibra and colleagues (2004) tested also 4-month-old infants, obtaining less clear results: the same general differences in the processing of the two stimuli were observed in infants as in adults, but with an opposite direction of effects as regards the relative changes of hoxy- and deoxy-haemoglobin. In infants hoxy-haemoglobin was found to decrease for faces, wherease deoxy-haemoglobin was found to increase for noise stimuli. More recently, Blasi, Fox, Everdell, Volein, Tucker, Csibra, Gibson, Hebden, Johnson and Ellwell (2007) tested with the same stimuli infants of the same age group (4 months) as those tested by Csibra and colleagues (2004). Blasi and colleagues (2007), however, used a more sophisticated NIRS equipment and targeting a wider group of brain regions. With such procedures, Blasi and colleagues (2007) obtained more convincing evidence of a grater activation for face than for noise stimuli. Among other things, this study demonstrated that the activation originated by the vision of the face stimuli affected a wider range of areas than that originated by the vision of the visually matched noise stimulus.

This relative abundance of neuroimaging data however, contrasts with the lack of behavioural data on preferences for faces when compared to visually matched noise stimuli, balanced in terms of the component spatial frequencies. Recently, this issue has been assessed in a study that tested human newborn babies[37] (Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, under revision). In this study we employed the same stimuli developed by Csibra, Henty, Volein, Ellwell, Tucker, Meek and Johnson (2004) in order to investigate behaviourally visual preferences of newborn human infants. We used a standard visual preference task in which two stimuli (a face and a visually matched noise stimulus) were simultaneously presented at the two sides of a fixation point and the duration of each trial was determined with an infant control procedure.[38] Newborns' visual preferences were then assessed analysing videotapes of their eye movements in order to extract the total looking time and the number of gaze orienting responses (discrete fixations) toward the two stimuli. Results obtained were very clear, showing, for both dependent variables considered, the presence of a significant preference for looking at the face stimuli with respect to the visually matched noise stimuli. This study thus demonstrates that newborns' preference for faces persists also when the role of component spatial frequencies is controlled for (in fact stimuli employed were matched in terms of the spatial frequency content). Results of this study are relevant also because they open the door to the investigation of the same issue (preference for faces with respect to frequency matched noise stimuli) using *naïve* domestic chicks, making it possible to employ a really comparative approach in the investigation of face preferences and to control for the role of previous visual experience with faces.

In consideration of the issues described above, we thus decided to run, as part of the work described in this thesis, a comparative study in order to be able to parallel in domestic chicks the behavioural evidence of spatial frequency-independent face preferences already obtained in newborns (Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, under revision).

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[37] Thirteen newborn babies were tested in this study

[38] When infants looked away from the experimental display for more than 10 consecutive seconds the trial ended and the experimenter started the next trial. In the second trial the left-right position of the stimuli was reversed. In this way infants were tested with 5 different pairs of stimuli, each consisting in a face and in a visually matched noise stimulus.

## Introduction to Experiments 6-9: Role of contrast polarity in face preferences

Adult human beings experience a marked difficulty when identifying a face from a photographic negative (i.e. a photographic image with reversed contrast polarity) or when the face is illuminated from below (Itier and Taylor, 2002; Johnston, Hill and Carman, 1992; see Itier and Taylor, 2004b for similar effects in children). Such effects are markedly reduced or even absent for object identification (Subramaniam and Biederman, 1997). The study of face sensitive ERP components, such as the N170, produced divergent results on this regard. In fact, contrast negation of visual stimuli modulates both the amplitude and the latency of the N170. If, on the one hand, the effect generated by contrast reversal on the amplitude of the N170 is nearly perfectly face-specific (i.e. not observed for non-face objects[39]), on the other hand the effect observed with regard to N170's latency is present also for stimuli other than faces (Itier, Latinus and Taylor, 2006)

The effect of contrast negation (i.e. reversal of contrast polarity) in face recognition is particularly remarkable because, in principle, a contrast negated image is exactly as informative as a normal image (i.e. an image presenting the normal direction of contrast polarity).

It has been theorised that this sensitivity to contrast polarity direction would be one of the hallmarks of face recognition (Biederman and Kalocsai, 1997). Contrast negation affects face recognition performance in a similar fashion with respect to face inversion (presentation of a face in an upside-down orientation)[40]. In fact both manipulations cause increased reaction times and false alarms, while decreasing hit rates, in a face recognition task (Itier and

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[39] With the notable exception of pictures of chairs that present an amplitude increase of the N170 when contrast is reversed. The amplitude increase observed for negative images of chairs is however smaller than that observed for faces.

[40] Terminological issue: The terms *reversal* and *negation* are here used to refer to manipulations of contrast direction that determine the presentation of images as negatives, whereas the term *inversion* does not refer to any manipulation of contrast direction, but is instead used to refer to the presentation of face stimuli upside-down (i.e. rotated of 180° on the vertical axis). The terms *reversal* and *negation* are always applied to the normal contrast polarity expected for a face stimulus, that under natural top-lit illumination should be composed of darker inner features on a lighter face background.

Taylor, 2002). Moreover, both contrast negation and face inversion (i.e. upside down presentation of the face stimulus) affect ERP components associated with this task in a similar fashion. In fact, face sensitive ERP components, such as the N170 and the VPP are enhanced and delayed by both inversion and contrast negation (Itier and Taylor, 2002). For a developmental study investigating the ontogenesis during childhood of face sensitive ERP components' sensitivity to contrast reversal, see Itier and Taylor (2004b).

Consistently with evidence indicating that contrast reversal elicits effects similar to those originated presenting faces upside down, it has been suggested that contrast reversal would disrupt configural processing of faces (Lewis and Johnston, 1997), in line to what theorized for faces presented upside down. In fact, when subjects have to judge if thatcherized faces are different from normal faces, RT increases if images are presented with negative contrast. Moreover, the detection of the displacement of face features is impaired by both inversion and contrast negation (Kemp, McManus and Pigott, 1990[41]). However, the impairment in configural processing caused by face inversion could be blarger than that caused by contrast reversal (Kemp, McManus and Pigott, 1990; see also Lewis and Johnston, 1997; please note that in Johnston, Hill and Carman, 1992, the impairment caused by face inversion was only slightly bigger than that of contrast reversal). Some form of configural processing could thus be preserved in negative images of faces. In fact, Hole, George and Dunsmore (1999) observed a chimeric-face effect (similar to the composite-face effect) for both normal faces and negative images of faces[42]. Hole and colleagues' (1999) data have been interpreted as an index of the fact that contrast negation would disrupt relational processing

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[41] Interestingly, this effect was not observed if schematic configurations composed of three blobs representing face features were employed instead of real faces. However, these schematic faces not only had their inner features replaced by three black blobs representing the eyes and the mouth, but lacked also of any face outline. When a face outline was added, the effect of negation reappeared (Kemp, McManus and Pigott, 1990).

[42] According to Hole, George and Dunsmore (1999) this would mean that negative faces should be equally effective as normal faces in activating the system specialized for face processing (i.e. face detection would be equally effective for normal and negative faces). However, this is in contrast with the evidence emerged in studies investigating face preferences in newborns using negative images of faces (e.g. Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005, see below) and also with evidence emerged in studies that directly investigated face detection (e.g. Lewis and Edmonds, 2003, see below).

used for face recognition, but leave intact holistic processing used for face detection (see also Itier and Taylor, 2002).

A further consideration is necessary when discussing the detrimental effects of contrast reversal in face recognition tests: in most cases subjects are asked to recognize faces in their negative versions after having first encountered them as positives. This could cause artifacts simply due the learning procedure employed. This issue was systematically investigated by Liu and Chaudhuri (1997), that explained impairment observed with negative faces as caused by the difficulty in matching 3D representations derived from negative faces to stored 3D representations originally derived from normal faces. However, this explanation does not apply to all the evidence available in the literature (e.g. Kemp, McManus and Pigott, 1990, discussed in Hole, George and Dunsmore, 1999; Kemp, Pike, White and Musselman, 1996).

In addition to the effects of contrast reversal on face recognition, Lewis and Edmonds (2003) investigated the effect of this manipulation (i.e. reversal of contrast polarity) in face detection. Contrast reversal resulted to impair face detection in adult human beings (in contrast to what suggested by Hole, George and Dunsmore, 1999). Moreover, the effect of contrast reversal was even larger than the effect of face inversion. This is in contrast to what observed in face recognition tasks where the impairment effect caused by contrast negation was, if anything, smaller than the impairment observed presenting faces upside down (see above). On the contrary, hue reversal impaired face detection much less than luminance reversal (Lewis and Edmonds, 2003). Thus, the presence of the correct direction of contrast polarity, regardless of face colour, may be a major factor in face detection in adult human beings. This, according to Lewis and Edmonds (2003), would be consistent with the idea of a face detection mechanism based on a template matching device (the template to be matched would consist in a luminance map). It is worth noting that this device proposed by Lewis and Edmonds (2003) is remarkably similar to the CONSPEC device hypothesised by Johnson (Morton and Johnson, 1991; Johnson, 2005).

Among the various interpretations proposed for the effects produced by contrast reversal, some emerge as being more relevant for the present discussion. According to one of the most influent hypotheses, face processing would be sensitive to contrast polarity reversal because this manipulation would reverse the interpretation of the luminance and shadow gradients that are employed to determine concavity and convexity in a smooth surface (i.e. it would compromise the “shape from shading” process) (Biederman and Kalocsai, 1997; Kemp, Pike, White and Musselman, 1996)[43]. Another popular interpretation of this effect would be that reversal of contrast polarity causes unusual pigmentation, and this would impair face recognition (Bruce and Langton, 1994; Vuong, Peissig, Harrison and Tarr, 2005). Recently Gilad and colleagues proposed that the destruction of a small set of stable 2D contrast polarity relationships might underlie the effect of contrast polarity reversal in human face recognition performance (Gilad, Meng and Sinha, 2009). In particular, these authors demonstrated that the presence of the normal polarity of contrast in the region surrounding the eyes (with the eyes being darker than the cheecks and the forehead, and the pupil darker than the sclera) is the crucial factor to determine face recognition. The interpretation proposed by Gilad, Meng and Sinha (2009) is that, due to the fact that these ordinal relationships are remarkably constant, they are incorporated in the facial representation used by the human brain for face recognition. Mismatches between such a representation and the perceptual input lead to impaired recognition. Reversal of the polarity of contrast (i.e. contrast negation) acts destructing these otherwise constant relationships. It is worth noting that, according to these authors, the crucial factor in determining normal face recognition is not the absolute magnitude of luminance of features in the eye region. What is crucial is the fact that the eyes have to be darker than the cheecks, and the pupil darker of the sclera, regardless of whether the eyes are two times or ten times darker than the cheecks, as long as the ordinal relationship among luminance of the various features is preserved (for works demonstrating that these ordinal relationships are a most informative feature in face processing see Balas and Sinha, 2006; moreover, a face detection mechanism developed by Viola and Jones, 2004 demonstrated that features comprising luminance relationships between eyes and their local neighborhood areas are most effective for classifying an image as a face). The implications of

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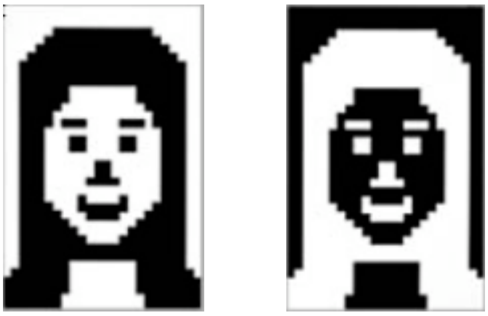
[43] Object identification on the contrary would be based on cues that are unaffected by contrast polarity, see Biederman and Kalocsai (1997).

the theory proposed by Gilad, Meng and Sinha (2009) and the details of their results will be further discussed below, in relation to convergent results obtained in the developmental literature.

In favour of the interpretation proposed by Gilad, Meng and Sinha (2009) there is also an experimental work of Liu, Collin, Burton and Chaudhuri (1999) showing that, even if images of faces lighted from below are difficult to recognize (possibly due to the abnormal luminance relationships among the eye region features), inverting the polarity of contrast of such images improves recognition (probably by re-creating the usual ordinal relationships among luminance of features in the eye region).

The presence of sensitivity to the inversion of contrast polarity in newborn babies has been object of some debate in the developmental literature (Dannemiller and Stephens, 1988; Mondloch, Lewis, Budreau, Maurer, Danemiller, Stephens and Kleiner-Gathercoal, 1999; Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). As already mentioned above, reversal of the direction of contrast polarity of face images, in fact, strongly decreases the recognition of such items as faces in human adult subjects (i.e. images with negative contrast polarity do not look nearly as face-like to adults as the normal images did). Thus, if newborns would be sensitive to contrast polarity, they should prefer a face displaying the normal direction of contrast polarity with respect to a face with a reversed direction of contrast polarity. The same line of reasoning predicts that infants should show a preference for a face-like stimulus with respect to a non face-like one if stimuli present the normal direction of contrast polarity, but this preference should disappear if stimuli are presented with negative contrast polarity. The first studies that investigated this issue in infants did not obtain evidence of a sensitivity to contrast negation up 12 weeks of age.

Dannemiller and Stephens (1988) investigated the preference displayed by 6- and 12-week old infants for a schematic face with respect to an identical stimulus with negative contrast polarity (i.e. the negative version of the face stimulus). Twelve-week olds, but not 6-week olds showed a preference to look at the face like stimulus with respect to its negative version. Mondloch and her colleagues (1999) replicated and extended this finding, comparing the preference of newborns, 6- and 12-week-olds for two schematic images of faces, using stimuli similar to those employed by Dannemiller and Stephens (1988). Also in this case one stimulus presented the normal contrast polarity expected for a face, having dark inner features on a white face background (Figure 23a), whereas the second stimulus presented reversed contrast (Figure 23b). A preference for orienting the gaze toward the stimulus with the appropriate direction of contrast was observed only in 12-week-old babies.



a b

Figure 23
This figure represents the two stimuli employed by Mondloch, Lewis, Budreau, Maurer, Danemiller, Stephens and Kleiner-Gathercoal (1999). Both configurations are schematic images of faces. Stimulus a) presents the normal direction of contrast polarity for a face (i.e. it has dark inner face features on a lighter face background); stimulus b) presents a reversed contrast polarity with respect to the natural appearance of a face, having lighter inner face features on a darker face background.

However, results obtained by Mondloch and her colleagues (1999) should be considered with caution, because the procedure that they employed differed markedly from the standard procedures used in similar studies in the literature. In fact, visual preferences expressed by newborns were determined subjectively, using any behavioural indicator available and chosen flexibly by the experimenters. Stimuli where shown to the babies as many times as necessary for the experimenter to form a hypothesis about whether each baby preferred one stimulus or the other.

The absence of significant effects proving sensitivity to reversal of contrast polarity in infants younger than 12 weeks, has been, in turn, subject to different speculations. According to some authors (e.g. Kleiner and Banks, 1987), results obtained by Dannemiller and Stephens[44] were in favour of the LSM (see the paragraph “Introduction to Experiment 5: Role of spatial frequencies composing stimuli in face preferences”). In fact, two images that are one the contrast reversed version of the other, have identical amplitude spectra but different phase spectra. Consequently, the LSM predicted no preference for one image over the other. On the other hand, Macchi Cassia, Kuefner, Westerlund and Nelson (2006a) interpreted the pattern of results reported by Dannemiller and Stephens (1988) and by Mondloch and her colleagues (1999), as being in favour of the perceptual narrowing hypothesis. In fact, the absence of a sensitivity to reversal of contrast polarity in younger babies and its subsequent appearance in older babies fits well with the idea of a progressive tuning of babies responses toward an increasingly well defined face category.

However, more recently and in contrast with the results described above, Farroni, Johnson, Menon, Zulia, Faraguna and Csibra (2005) obtained convincing evidence of sensitivity to the direction of contrast polarity in newborn babies, using a standard visual preference task (infant control technique). They demonstrated (Experiment 1a) that newborns preferred to look at a schematic face-like stimulus with respect to a non-face-like one only if stimuli presented the normal direction of contrast polarity (i.e. had darker inner features on a lighter face background, Figure 24, a and b). On the contrary, this preference disappeared if the two stimuli had negative contrast polarity (i.e. lighter inner features on a white background, Figure 24, c and d).

Farroni and her colleagues were also able to restore the original preference for the face in a pair of stimuli with negative contrast polarity. They obtained this result by restoring the normal direction of contrast polarity, but limitedly to inner face features (Experiment 1b, Figure 24, e and f). That is to say that they added a black dot within the white inner face features of the negative images. In this way, the face-like stimulus presented again a triangular configuration of dark elements (the black dots) on a lighter background (in this case the lighter

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[44] Please note that even if the paper of Dannemiller and Stephens is dated 1988, Kleiner and Banks were already aware of the content of this paper when they were publishing their work in 1987, possibly because the paper of Dannemiller and Stephens was already in press at that moment. In fact, in 1987 Kleiner and Banks quoted the paper of Dannemiller and Stephens as “in press”.

background was constituted by the three white squares that represent the inner features of the stimuli).

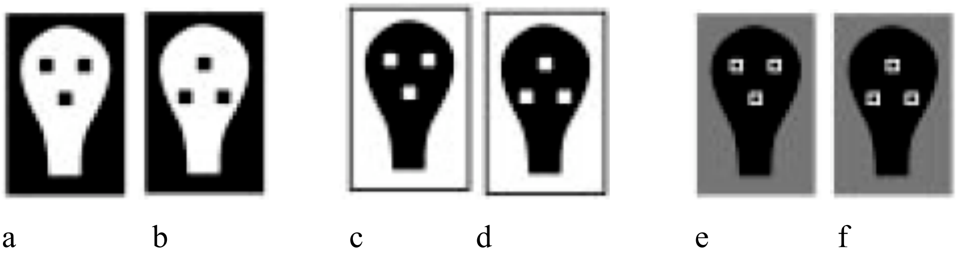

Figure 24
Reproductions of the schematic stimuli employed by Farroni, Johnson, Menon, Zulia, Faraguna and Csibra (2005) in their Experiment 1. In the first pair of stimuli (a and b) both configurations present the normal direction of contrast polarity expected for a face. In the second pair of stimuli (c and d) direction of contrast polarity has been reversed. Finally, in the third pair of stimuli (e and f) a pupil-like dot has been added within each white inner feature. Stimuli a), c) and d) present a face-like configuration of inner features, whereas stimuli b), d) and f) can not represent faces.

The interpretation that Farroni and her colleagues give of this later result (i.e. the reappearance of the preference for the face stimulus as a consequence of the introduction of the pupil-like black dot) is based on their view about the adaptive role of newborns' face preferences. In fact, they argument that: "…*if the function of newborns' orientation bias is to establish eye contact, and human eyes are identified as dark spots within lighter areas (Kobayashi and Kohshima, 1997), placing dark "irises" within the white squares in the negative polarity images should bring the preference for upright images back*" (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005).

The general interpretation that these authors give of their results is based on a functional approach to visual preferences displayed by newborns. According to this approach, a mechanism or a bias of whichever nature is called "face relevant" if it is efficient in drawing infants' attention to faces in a natural environment. This functional approach predicts that newborns' preferences for faces would be influenced by contrast polarity. In fact: "*If the mechanisms that bias newborns' orientation to stimuli has been selected to find faces in a* *natural environment under natural (top-down) illumination (i.e., the function is face detection), it should also be sensitive to the light-shadow pattern generated on faces by such conditions. In particular, the eye and mouth regions are recessed on a face and therefore appear to be darker than other parts of the face that are directly illuminated… If the newborns' visual biases evolved to help them locate faces in a natural environment, infants should show no preference for face-like patterns where the elements within the face are lighter than the background, because those elements would indicate protrusions rather than recesses for their visual system*" [45] (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005).

A further test of this hypothesis was conducted in three further experiments that employed photographic images of real faces as test stimuli (see Figure 25). With this procedure it was possible to demonstrate that the above described findings hold also for more naturalistic stimuli. In fact a preference for an upright face with respect to a face whose inner features were rotated of 180° was observed for stimuli having the normal direction of contrast polarity (Figure 25, a and b), but not for stimuli having negative contrast (Figure 25, c and d) (Experiment 2a, Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). Moreover, a further experiment (Experiment 2b) demonstrated that newborns preferred to look at a face illuminated from above (Figure 25e) (i.e. consistently with natural illumination usually occurring in the ancestral environment of our species) with respect to a face illuminated from below (Figure 25f). This evidence strongly points toward the hypothesis that sensitivity to contrast polarity is an effect originated by a mechanism evolved in order to detect faces as they appear under natural top-lit illumination.

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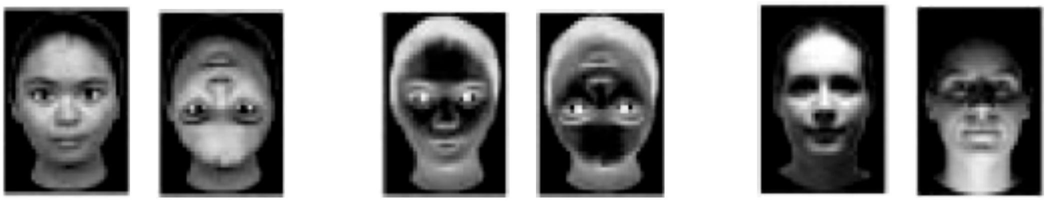
[45] Please note that a very similar argumentation holds also for chicks' and hens' faces (see Figure 7). In fact, the dark eyes of a hen are visible from a frontal view, so is the shadow created by the bill.



a b c d e f

Figure 25

Reproductions of the schematic stimuli employed by Farroni, Johnson, Menon, Zulia, Faraguna and Csibra (2005) in their Experiment 2. In the first pair of stimuli (a and b) both configurations present the normal direction of contrast polarity expected for a face. In the second pair of stimuli (c and d) direction of contrast polarity has been reversed. Stimuli a) and c) represent a human face, whereas stimuli b) and d) can not represent faces, because inner face features have been rotated of 180° within the face outline. Stimuli e) and f) both represent a human face, but stimulus e) is illuminated from above, whereas stimulus f) is illuminated from below.

An additional reason of interest for the study of Farroni and her colleagues (2005) is that these authors were able to contrast predictions originated by their functional account of newborns' face preferences with predictions originated by theories that explain face preferences as a result of simple domain-general attentional biases (e.g. the up-down bias, Turati, Simion, Milani and Umiltà 2002; Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002). In fact, according to theories that explain newborns' face preferences as due to non-face-specific attentional biases (such as the up-down bias theory), there should be no difference in preferences observed with pair of stimuli that differ in the contrast polarity, as long as they do not differ in the distribution of high-contrast inner features. Farroni and her colleagues even argument that the up-down bias theory should predict a higher preference for faces when stimuli have negative contrast polarity, because the high contrast elements present in the upper part of the face stimulus "*may appear to be closer to the observer in relation to a background surface*".

Finally, the results obtained by Farroni and her colleagues (2005) are relevant because they offer evidence in favour of a crucial role of eyes in eliciting face preferences and in modulating the effect of contrast polarity (Experiment 1b, see above). Farroni and others explain this finding as due to a bias toward potentially communicative partners, in line with evidence that newborns preferentially orient toward faces with open, as opposed to closed, eyes (Batki, Baron-Cohen, Wheelwright, Connellan and Ahluwalia, 2000). Please note that, also in adult human beings, face detection performance depends mainly on the visibility of the eyes (Lewis and Edmonds, 2003).

This central role of the eyes is in line also with evidence obtained in a study (briefly mentioned above) that investigated the role of contrast polarity in face recognition by adult human beings (Gilad, Meng and Sinha, 2009). These authors demonstrated that face recognition is mainly influenced by ordinal relationships between luminance levels of areas surrounding the eyes, by employing as stimuli a set of “contrast chimeras” (faces that are photo-negatives except in the eye region, see Figure 26).

Figure 26
Reproductions of the stimuli employed by Gilad, Meng and Sinha (2009). Stimuli in the first row (a) are standard images of faces with reversed contrast polarity. Stimuli in the second row (b) are the contrast chimeras in which the normal direction of contrast polarity has been restored for the eye-region only.

Recognition performance for the contrast chimeras was significantly higher than for negative images and similar to that observed for normal photographic images of human faces (with natural unaltered contrast polarity). Moreover, activation of the FFA (Fusiform Face Area, a region which is considered to be specialized in face processing, especially in the right hemisphere, Kanwisher, McDermott and Chun, 1997) was proved to be reduced for negative images of human faces, but not for the contrast chimeras (activation observed for the contrast chimeras was in fact indistinguishable from that observed for normal images of human faces).

Finally, Gilad, Meng and Sinha (2009) demonstrated that contrast chimeras in which the mouth region, instead of the eye region, was restored in its natural contrast polarity were not effective in improving face recognition performance. The effect they observed was thus specific of the eye region.

Evidence indicating a main role of the eyes in the processing of negative images of faces, was also obtained by Itier, Alain, Sedore and McIntosh (2007). These authors demonstrated that the increased amplitude of the N170 recorded for negative faces reflected the processing of the eyes. Similarly, results obtained by Itier, Latinus and Taylor (2006) when investigating the role of contrast reversal in modulating the face-specific ERP component N170, seemed to indicate that effects of contrast reversal on the amplitude of this component reflected mainly the contribution of the eye region. This would seem in line with the argumentation reported by Gilad, Meng and Sinha (2009) about the central role of the eye region in contrast reversal effects. However, the conclusion that Itier, Latinus and Taylor (2006) obtain from their results is that negative images of eyes would be processed like normal positive eyes. The rationale of this argumentation is that the increase in amplitude observed for the N170 with negative images of faces would be due to the recruitment of neurons responding to the eye region of a face. Such neurons would not respond to eyes when eyes are embedded in a normal face configuration (i.e. presented within an upright face having a positive contrast polarity), possibly because configural processing of the face would inhibit the processing of isolated features. Manipulations such as negation or inversion would impair the configural processing, thus allowing the isolated processing of eye features.

Despite discrepancies in the interpretations proposed by different authors, it seems however clear that eyes play a relevant role in the processing and perception of negative faces in both newborn babies and human adults (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005; Gilad, Meng and Sinha, 2009; Itier, Latinus and Taylor, 2006).

On the basis of all the evidence described above, we decided to run a series of experiments aiming at investigating the role of contrast polarity reversal in chicks' preferences for schematic faces. Our aim in doing so was also to try to parallel the results obtained by Farroni, Johnson, Menon, Zulian, Faraguna and Csibra (2005) on newborn babies, tracing a further comparison between the two species.

## General materials and methods

### *Subjects*

Subjects were male and female domestic chicks (*Gallus gallus domesticus*) of the “Hybro” strain (a local strain derived from the White Leghorn breed). Fertilized eggs were obtained weekly from a local commercial hatchery (Agricola Berica, Montegalda, VI, Italy) on the 14th day of incubation. Eggs were incubated (in a MG 70/100 Rurale incubator) from Days 14 to 17. On the 17th day of incubation eggs were placed in a hatchery (MG 100). During incubation and hatching eggs and chicks were maintained in complete darkness.

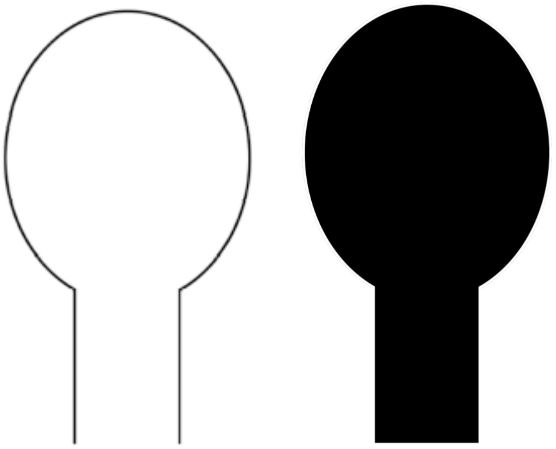
Each chick was tested only once (thus each chick participated to only one experiment and was exposed to only one pair of stimuli).

After testing chicks were immediately caged in groups with food and water available *ad libitum*. Moreover, soon after that chicks were donated to local farmers.

### *Rearing conditions*

After hatching chicks were immediately placed singly in metal home-cages (28 cm × 16 cm x 40 cm) whose walls and floor were lined with white opaque paper. The cages were lit (24 h/day) by 36 W fluorescent lamps (placed 15 cm above the cages). Chicks were maintained at a controlled temperature (c. 28–31 °C) and humidity (c. 70%), with water available *ad libitum*. At the beginning of the first day of life, some food was scattered over the floor in each cage.

Except in Experiment 5, an artificial imprinting object was present in each cage. It consisted of a simple shape, representing a featureless face printed on orange cardboard paper (Figure 27, a and b). The imprinting object was identical in shape and outline to the experimental stimuli that were employed later at test. It was 10 cm high and 5.6 cm large (on the point of maximum width). The imprinting object was placed upon one of the walls in each cage, with its lower boundary (the base of the “neck”) adjacent to the cage floor, so that the round-shaped upper part of the stimulus (the “face”) was presented at about the height of the sight-line of a standing newborn chick. This procedure did not provide chicks with any information regarding the internal features of a face, but increased the likelihood that subjects would perform the experimental task at test. At test, in fact, chicks had to approach one of two stimuli that were both equally similar to their imprinting object.



a b

Figure 27

Figure a) represents the imprinting object employed in Experiments 1-4; Figure b) represents the imprinting object employed in Experiments 6-11. Both imprinting objects, including the stimulus b), were printed on a cardboard paper of a light orange colour.

Special precaution was taken in order to avoid chicks received any visual experience concerning the structure of the internal features of a face, prior to the moment of the test. In particular, chicks never saw the experimenter's face or the face of another chick. Whenever required chicks were manipulated in complete darkness. If it was necessary to transport the chicks in illuminated environments, this was performed maintaining each chick inside a closed cardboard box. Manipulation of the chicks for sexing and daily care was performed only after covering the chick's head or eye region, preventing it from any possible visual experience.

***Apparatus***

The test apparatus (Figure 28) consisted of a white-plywood longitudinal runway, from now on named the 'choice-runway', with two experimental stimuli being presented at the two opposite ends. The choice runway was divided into three virtual sectors: a central area that was equidistant from the two experimental stimuli, and two side-areas, each of them adjacent to one of the two stimuli. Each side-area ended with a translucent glass screen. The two stimuli were placed upon these glass partitions. Each stimulus (and therefore also the inside area of the choice runway) was lit by a 40 W lamp placed beyond the glass partition, while the rest of the experimental room was maintained in darkness. The two stimuli were placed upon the glass partitions so that their lower boundary (the base of the “neck”) was at the same level as the runway floor, and the round-shaped upper part of the stimulus (the “face”) was in line with the eyes of a chick standing in the apparatus. The dimensions of the apparatus were as follows: choice-runway 45 cm x 22.3 cm large, 30 cm high; central sector 15 cm long; two lateral sectors 15 cm long each. A video camera was placed above the apparatus, to record chicks’ behaviour during the test. The camera was also connected to a monitor screen in the same room, enabling the experimenter to score behaviour on-line during test, without disturbing the animal.

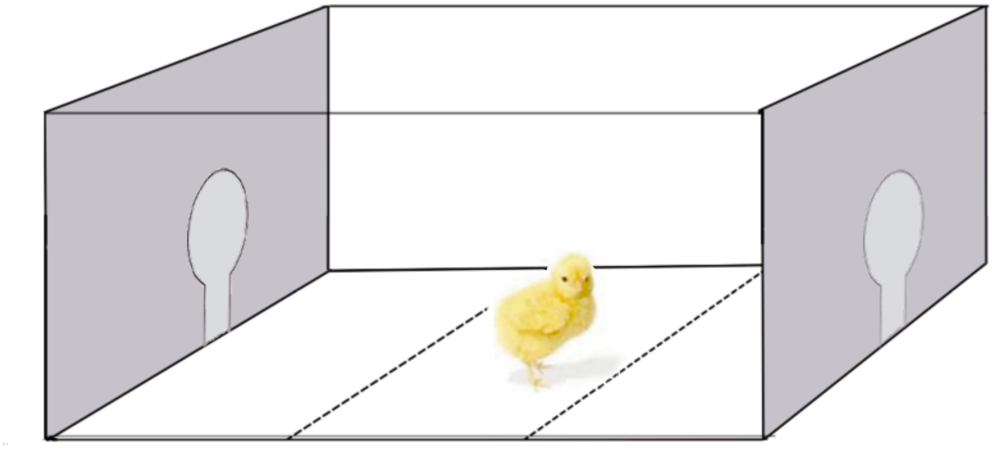


Figure 28

Schematic representation of the testing apparatus (‘choice runway’) and of its division into three virtual sectors. The chick is represented within the central sector, equidistant from the two glass screens (represented in grey in this image), on which test stimuli were positioned during the test. For illustrative purposes stimuli positions are marked by two lighter shaded areas on the glass screens.

### *Test stimuli*

A different pair of test stimuli was employed in each experiment. A detailed description of test stimuli will be given for each experiment independently. However, with the only exception of Experiment 5, all test stimuli were identical to the imprinting object (described above) in colour, overall shape and dimensions (test stimuli, except for Experiment 5, were printed on the same cardboard paper of a light orange colour used for the imprinting objects). The only difference between test stimuli and the imprinting object was the presence, in each test stimulus, of three square blobs (0.9 x 0.9 cm) representing the stimuli internal features. Note that 2-day old chicks are characterized by an excellent visual acuity, which would certainly allow them to discriminate the internal elements of our test stimuli (Schmid and Wildsoet, 1998).

In Experiments 1-4 the blobs representing stimuli inner features were darker than the stimuli background (see e.g. Figure 29), whereas in Experiments 6-11 the square blobs were lighter than the stimuli background (see e.g. Figure 34).

In Experiments 1-4, the disposition of the square blobs representing stimuli inner features was varied in each experiment. Moreover, the two stimuli employed for each experiment differed only from one another in the position of the square blobs. This was done in order to investigate the roles of facedness and top-heaviness in determining chicks' preferences.

In Experiments 6-11, the two stimuli composing each pair differed from one another in the disposition of their inner features, but the disposition of the inner features was always the same in all pairs of stimuli used in the various experiments. In fact, stimuli were negative images obtained reversing the direction of contrast polarity of stimuli employed in Experiment 1. In Experiments 6-11 stimuli were manipulated in order to alter the contrast relationships between inner features and stimuli background. This was done in order to investigate the effect of contrast reversal on chicks' face preferences.

Finally, in Experiment 5 stimuli consisted in a colour photographic image of a human face and a visually matched noise stimulus, that was a scrambled stimulus digitally obtained in order to contain the same spatial frequencies, colour and luminance distribution of the face stimulus (see Figure 33). This was done in order to be able to parallel evidence obtained with newborns' using the same stimuli and to investigate the role of spatial frequencies composing stimuli in chicks' face preferences. An additional advantage was that these stimuli allowed us to test whether chicks' face preferences would be non-species-specific (i.e. extended to faces of other species) as suggested by some former evidence (e.g. Johnson and Horn, 1988), in line with the presence of a very broad template for the detection of faces.

***Procedure***

The test was performed on the second day of life. The imprinting stimulus was removed from each cage 20 minutes before the beginning of the test. Each subject was carried, in a closed cardboard box, to the experimental room (located near the rearing room, and kept at 29-30° C with a humidity of 68%), where the chick was placed directly in the central area of the test apparatus. The chick's position at the starting point with respect to the test stimuli, as well as the position of the two stimuli within the apparatus, was balanced across animals.

Chicks' behaviour was recorded for a total of 6 consecutive minutes. If the chick remained in the mid compartment this indicated no choice, whereas entrance and permanence of the chick in one of the side compartments was regarded as a preference for the object placed at that end of the runway (see Vallortigara and Andrew, 1991 for initial validation of these procedures). A computer-driven event recorder allowed the experimenter to score the time (seconds) spent by the chick in each of the three areas during the overall test period.

Behavioural measures considered were:

- first stimulus approached by each chick (i.e. the first side sector entered during test);
- latency of first approach (i.e. the time required to leave the centre of the apparatus for the first time during the test);
- proportion of time spent near the face-like stimulus (i.e. the proportion of time spent in the lateral sector adjacent to the face-like configuration, during the whole length of the test, with respect to the time spent in both side sectors).

All measures were scored with a blind procedure: the scorer was in fact a student unaware of the aims of the research conducted.

***Data analysis***

To compare the number of chicks that approached first the face-like or the non-face-like configuration (the top-heavy and bottom-heavy configuration in Experiment 2) we used the chi-square test of independence. Whenever it was necessary to add a further factor to that analysis (e.g. in order to compare the number of chicks that approached the face-like or non-face-like stimulus in imprinted versus not imprinted chicks, in Experiment 1), the chi-square test of independence was applied on a 2 x 2 contingency table.

To represent the proportion of time spent near the face-like stimulus, an index was calculated from the time spent into the two lateral sectors using the formula:

$$\left(\text{Time by the face-like stimulus} \;/\; \text{Time by the face-like stimulus} + \text{Time by the non-face-like stimulus}\right) \times 100$$

Significant departures from chance level (50), which indicated a preference for the face-like (> 50) or non-face-like stimulus (< 50), were estimated by one-sample two-tailed *t*-test.

The latency to approach one stimulus for the fist time during the test was analysed comparing latencies of chicks that approached the face-like or the non-face-like stimulus (the top-heavy and bottom-heavy configuration in Experiment 2), using and independent-sample *t*-test.

## Experiment 1

The aim of the first experiment was to investigate whether a spontaneous preference for schematic face-like configurations would be present (prior to any visual experience regarding the structure of faces' inner features) in newly-hatched domestic chicks, when the role of the up-down bias is controlled for. Chicks' preferences were thus tested between two top-heavy stimuli, only one of which represented a face.

### *Subjects*

Subjects were 138 (69 male and 69 female) domestic chicks (*Gallus gallus domesticus*).

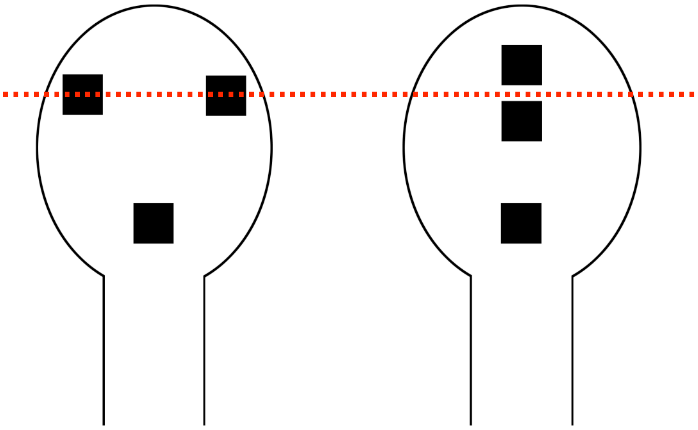
A sub-sample of 104 chicks (52 male and 52 female) out of the 138, was reared in exactly the same conditions as described in the "General materials and methods", but in the absence of any imprinting object. This procedure was applied in order to test the effect of the presence of an imprinting object on chicks' face preferences. Subjects employed in all further experiments were always reared in the presence of the imprinting object, except in Experiment 5.

### *Test stimuli*

The two test stimuli (see Figure 29a, b) employed in Experiment 1 were top-heavy configurations (having 2 elements in their upper part and 1 in their lower part), similar to those used by Turati, Simion, Milani and Umiltà (2002), in their Experiment 2. Moreover, the average height of the blobs representing the internal features in either the upper or lower parts of the stimuli was identical for the two configurations. However, contrary to stimuli used by Turati, Simion, Milani and Umiltà (2002, second experiment), both configurations were symmetrical on the vertical axis (in the second experiment run by Turati and her colleagues only the face-like stimulus was symmetrical). In this way we controlled for the role of properties such as top-heaviness and vertical symmetry in chicks' face preferences. In order to test for the role of *facedness* in chicks' preferences, only one of the two configurations represented a face. In this way we were able to contrast the predictions of the up-down bias theory (Turati, Simion, Milani and Umiltà, 2002) and of the of the CONSPEC-CONLERN model (Morton and Johnson, 1991; Johnson, 2005). In fact, if chicks' preferences were driven by *facedness*, as predicted by the CONSPEC-

CONLERN model proposed by Johnson, a preference for the face-like configuration would be expected (Figure 29a). On the contrary, according to the up-down bias theory proposed by Turati and colleagues no preference should emerge, because both stimuli are top-heavy configurations.

The blobs in the face-like configuration were arranged in such a way as to compose an upside down triangle. This general configuration roughly corresponds to that of a hen or of a chick face (as well as of a human face) in frontal view, when under natural (top-lit) illumination (see Figures 1 and 7). The two upper black blobs of the face-like stimulus could correspond to the eyes of the hen or of a sibling chick, whereas the lower blob could correspond to the bill and to the shadowed area beneath it. On the other hand, all the three blobs present in the non-face-like configuration were aligned along the same vertical axis, so that the configuration could not possibly resemble a face. Test stimuli were inspired by configurations that had been used previously in studies on preferences for face-like displays in human newborns (Morton and Johnson, 1991, for a review), but adapted to increase their resemblance to the face of a hen (our stimuli had a rounder outline, a more pronounced neck and eyes positioned more temporally with respect to those usually employed with infants).



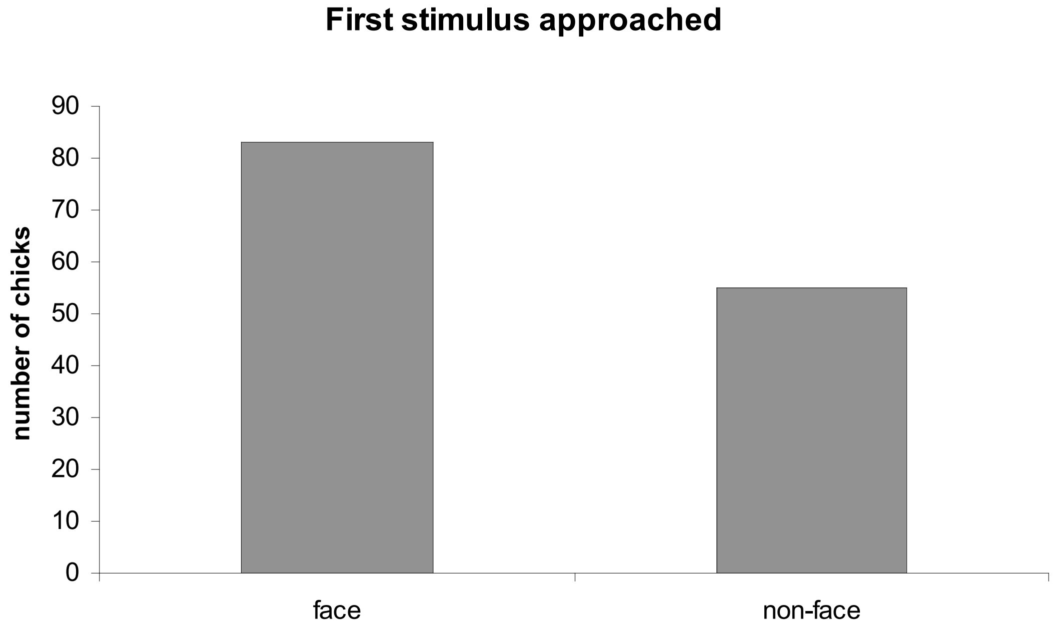
a b

Figure 29

Representation of the two stimuli used in Experiment 1. Stimulus a) represents a face-like configuration, whereas stimulus b) is a non-face-like configuration. Both stimuli are equally top-heavy and symmetrical along the vertical axis. The red dotted line was not present on original stimuli, and was here added on the purpose of illustrating that the average height of the blobs representing the internal features in the upper part of the stimuli was identical for the two configurations.

### *Results*

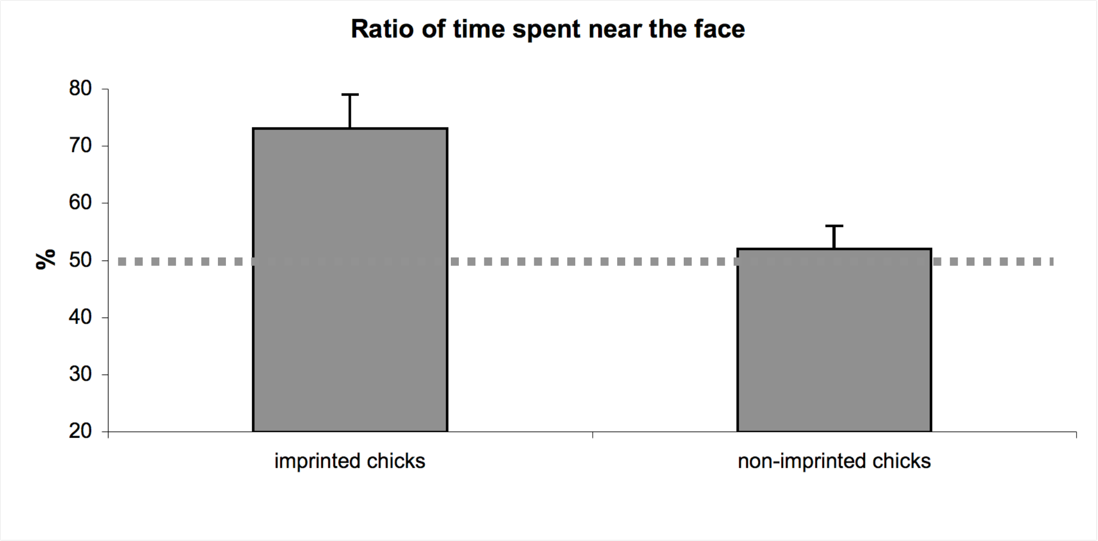
As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the face-like or the non-face-like configuration as first stimulus did not significantly differ between imprinted and non-imprinted subjects ($\chi^2_1 = 2.053$; $p = 0.152$; 24 “imprinted” chicks approached the face and 10 the non-face; 59 “non-imprinted” chicks approached the face and 45 the non-face). Thus, the number of chicks approaching the face-like and the non-face-like stimulus when leaving the centre of the apparatus for the first time during the test was directly compared for the overall sample. Overall, the number of chicks that approached the face-like configuration as the first stimulus was significantly higher than the number of chicks that approached the non-face-like configuration ($\chi^2_1 = 5.681$; $p = 0.017$). Thus, overall, chicks showed a preference for approaching the face-like stimulus first, when leaving the centre of the apparatus for the first time during the test. See Graph 1.



Graph 1

Number of chicks approaching the face-like (left hand side) versus the non-face-like configuration (right hand side) as first stimulus during the test in Experiment 1.

On the contrary, the ratio of time spent near the two stimuli was significantly different between imprinted and non-imprinted chicks ($t_{136}$ = 2.626, p = 0.010). See Graph 2



Graph 2

Mean proportion of time spent near the face-like stimulus in Experiment 1, for "imprinted" (left hand side column) and "non-imprinted chicks" (right hand side column). Group means with SEM are shown. The dotted line represents chance level.

The ratio of time spent near the face-like configuration was thus compared to chance level independently for imprinted and non-imprinted chicks. This comparison was significant for imprinted chicks ($t_{33}$= 3.525; p = 0.001, see Graph 2), but non significant for non-imprinted chicks ($t_{103}$ = 0.542; p = 0.589). Thus, imprinted chicks spent significantly more time near the face-like configuration than expected by chance level.

Latency to approach of imprinted chicks[46] was compared between chicks that approached the face-like and the non-face-like stimulus when leaving the centre of the apparatus for the first time during the test. This comparison was not significant ($t_{32}$ = -0.240; p = 0.812). Thus chicks that approached the face-like stimulus were not significantly quicker in doing so than chicks that approached the non-face-like one.

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[46] Due to technical problems in data collection this dependent variable was not available for non-imprinted chicks.

### *Discussion*

In this experiment chicks showed a spontaneous preference for a face-like configuration with respect to a stimulus matched for its top-heaviness (i.e. presenting the same number of elements in its upper part). Thus, visually inexperienced chicks preferred a schematic stimulus representing the structure of a face with respect to a similar top-heavy configuration that lacked the *facedness* property. This finding is consistent with the model proposed by Morton and Johnson (1991; Johnson, 2005), claiming that the preference of chicks would be guided by an innate representation (CONSPEC) attracting chicks' attention toward stimuli whose internal features are arranged according to a triangular face-like structure.

On the other hand, our results are not consistent with those obtained by Turati, Simion, Milani and Umiltà (2002, second experiment), that showed that human newborns did not exhibit any preference between a face-like and a non-face-like configuration, when both of them were top-heavy stimuli. One possible explanation for this could be found in differences in symmetry between the stimuli used here and those used by Turati and her colleagues (2002). In the present experiment both the face-like and the non-face-like configuration were symmetrical along the vertical axis. On the contrary, the stimuli used by Turati and others differed not only according to the property of *facedness*, but also in their symmetry. Since symmetry is an important structural property of a stimulus, it is possible to hypothesize that this could have influenced the results obtained (e.g. asymmetrical stimuli could be more difficult to be processed and thus require additional attentional resources, Bornstein, Ferdinandsen and Gross, 1981; Fisher, Ferdinandsen and Bornstein, 1981; for a discussion of this issue see the paragraph "Introduction to Experiments 1-4: Role of vertical asymmetry of inner facial elements in face preferences"). The reasons for the discrepant results obtained here in chicks with respect to the results obtained by Turati, Simion, Milani and Umiltà (2002) in newborns will be discussed in detail in the "General discussion of Experiments 1-4".

A sample of our chicks was imprinted on a stimulus representing a "featureless face", whose outline was identical to that of the test stimuli, but lacking any internal feature. Even if this procedure could not have provided chicks with any information regarding the internal features of a face (and thus with a bias in favour of one of the test stimuli), it is all the same interesting to question whether a preference for the face-like stimulus could also be present in chicks not exposed to the “featureless face”. Results from the sample of chicks not exposed to any imprinting stimulus during rearing, demonstrated that this was the case. Interestingly, however, in contrast to the chicks exposed to the featureless face, non-imprinted chicks seemed to lose interest in the face-like stimulus, after the initial choice. It is likely that this reduction in interest for the preferred stimulus, which was observed only in this sample of chicks, was due to the fact that these subjects were lacking in experience of any conspicuous visual object and could have had a slightly altered social behaviour, including a less sustained interest in social stimuli. The presence of conspicuous objects is normally part of a chick’s natural environment. Moreover, this result is also consistent with previous literature showing the role of non-specific experience, such as “priming” visual input, in the preference for conspecific-like objects (Bolhuis, Johnson and Horn, 1985, see paragraph “Presence of an unlearned representation of social object in chicks”). The exposure to the outline lacking any features seems therefore to represent a more reliable and ecologically valid procedure and was maintained in all subsequent experiments (with the only exception of Experiment 5).

## Experiment 2

The results obtained in Experiment 1 do not allow any inference regarding the presence of an up-down bias *per se* (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002) in visually inexperienced chicks. It could be that any preference for top-heavy configurations is completely absent in chicks. If this species has evolved a representation for the innate recognition of faces (the triangular arrangement of features detected by CONSPEC), any other broad kind of bias (such as that for top-heavy configurations) would be useless for the detection of conspecifics. On the other hand, it could also be hypothesized that the up-down bias is present also in chicks, but that it coexists with a stronger preference for a CONSPEC-like kind of representation, or that the up-down bias could be found in chicks as a by-product of the preference for CONSPEC-like stimuli (due to a generalization of the innate preference for configurations presenting some face-like properties, such as top-heaviness). These issues will be in part explored in Experiment 2.

### *Subjects*

Subjects were 62 (31 male and 31 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

The test stimuli used in Experiment 2 were identical to those used in the previous experiment except for the position of the three square black blobs. The configurations used for this experiment resembled those employed by Turati, Simion, Milani and Umiltà (2002, first experiment). Both stimuli were non-face-like configurations, but one was a top-heavy stimulus (Figure 30a), whereas the other was a bottom-heavy configuration (Figure 30b).

In this way we were able to test whether, in the absence of any face-like configuration, it was possible to obtain any preference for a non-face-like top-heavy stimulus, as predicted by the up-down bias theory (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà). It should be noticed that the CONSPEC-CONLERN model (Morton and Johnson, 1991; Johnson, 2005), is on the contrary neutral with regard to the results of the present experiment. In fact, no direct prediction is advanced by such a model with regard to the preferences of newborn vertebrates for non-face-like stimuli. According to the model proposed by Johnson, it is possible to hypothesise either that no preference should be observed, due to the fact that none of the stimuli represents a face, or that the top-heavy stimulus should be preferred over the bottom-heavy one, because it presents at least one of the properties that characterizes faces.

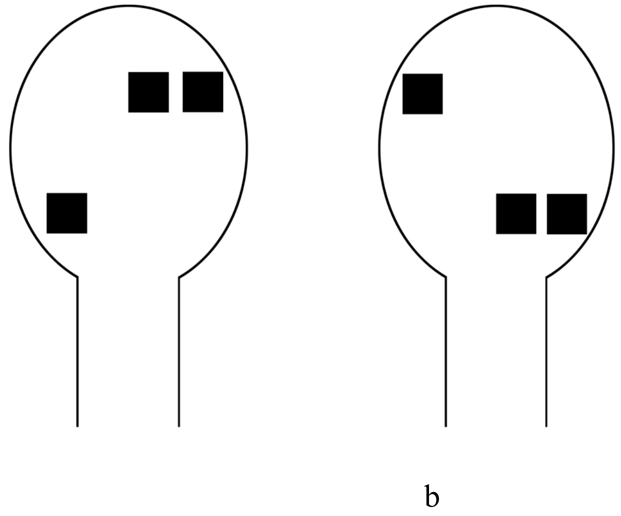


Figure 30
Representation of the two stimuli used in Experiment 2. Stimulus a) represents a top-heavy configuration, whereas stimulus b) is a bottom-heavy configuration. Both stimuli are non-face-like configurations.

### *Results*

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the top-heavy configuration as first stimulus did not differ from the number of chicks that approached the bottom-heavy configuration ($\chi^2_1 = 0.000$; $p = 1.000$). In fact, exactly the same number of chicks approached the top-heavy and the bottom-heavy stimulus when leaving the centre of the apparatus for the first time during the test.

Moreover, in line with the above mentioned result, the proportion of time spent near the top-heavy stimulus for the whole length of the test did not differ significantly from what expected by chance ($t_{61} = -0.586$; $p = 0.560$).

Finally, as regards the latency to approach one stimulus for the first time during the test, no significant effect of the first stimulus approached was observed ($t_{60} = -0.671$; $p = 0.505$). This meant that chicks were not significantly quicker when approaching the top-heavy or the bottom-heavy stimulus.

Overall, results of the present experiment did not reveal any significant effect (i.e. no index of a preference for one of the two stimuli employed emerged).

### *Discussion*

In this second experiment visually inexperienced chicks did not demonstrate a preference for non-face-like top-heavy configurations with respect to similar bottom-heavy configurations, in contrast with the results reported by Turati, Simion, Milani and Umiltà (2002) in human newborns. This suggests that, if no face-like configuration is present among test stimuli, an up-down bias can not be found in chicks. A difference in visual acuity between the lower and upper visual fields has been hypothesized to be the cause of the up-down bias in newborns (see the paragraph “Introduction of Experiments 1-4: Role of vertical asymmetry of inner facial elements in face preferences”). Chicks also show a difference in visual acuity in the upper visual field with respect to the lower visual field (Hodos and Erichsen, 1990). Thus, the lack of any up-down bias in chicks challenges the hypothesis that the presence of a different visual acuity in correspondence of upper or lower visual field could explain the bias in human newborns. Some possible interpretations of the differences in the results obtained in chicks with respect to human newborns will be considered in the “General discussion of Experiments 1-4”.

## Experiment 3

The aim of the present experiment was to check whether visually inexperienced chicks would maintain their preference for schematic face-like stimuli (Experiment 1) when this preference is put in conflict with the hypothetical influence of the up-down bias (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002). In order to do so, we tested chicks' spontaneous preference for a bottom-heavy face-like stimulus with respect to a top-heavy stimulus not representing a face (see Figure 31, a and b).

### *Subjects*

Subjects were 44 (23 male and 21 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

The test stimuli employed in Experiment 3 were identical to those used in the previous experiments, except for the position of the three square black blobs (see Figure 31, a and b). In the present experiment, in fact, stimuli consisted of one top-heavy configuration and one bottom-heavy configuration. The stimuli internal features were arranged so that the bottom-heavy configuration represented a face-like display with its features located in the lower part of the face, whereas the top-heavy configuration represented a non-face-like display with its features located in the upper part of the face (see Figure 31, a and b). These two stimuli were inspired by the configurations used by Turati, Simion, Milani and Umiltà (2002), but they were slightly altered according to the schema, recently proposed by Johnson (2005, see Figure 1), of an optimal pair of stimuli to contrast the up-down bias theory with respect to the CONSPEC-CONLER theory. The main difference between Turati and others' stimuli and the pair of stimuli used in the present experiment is that in our stimuli the two blobs representing the "eyes" of the face-like configuration were placed at the same height as the corresponding blobs in the non-face-like configuration (i.e. the two configurations differed only for the position of the third blob, either in the upper or lower part of the stimulus).

With these stimuli we were thus able to directly contrast the predictions advanced by the up-down bias theory (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002) and the CONSPEC-CONLERN model (Morton and Johnson, 1991; Johnson, 2005). In fact, if a putative up-down bias (of whose presence, however, we did not obtain any evidence form the previous experiments) would be responsible for chicks' face preferences, in the present experiment chicks' should show a preference for the top-heavy stimulus not representing a face. On the contrary, if a CONSPEC-like mechanism would drive chicks' preferences, we should observe a preference for the bottom-heavy face-like stimulus.

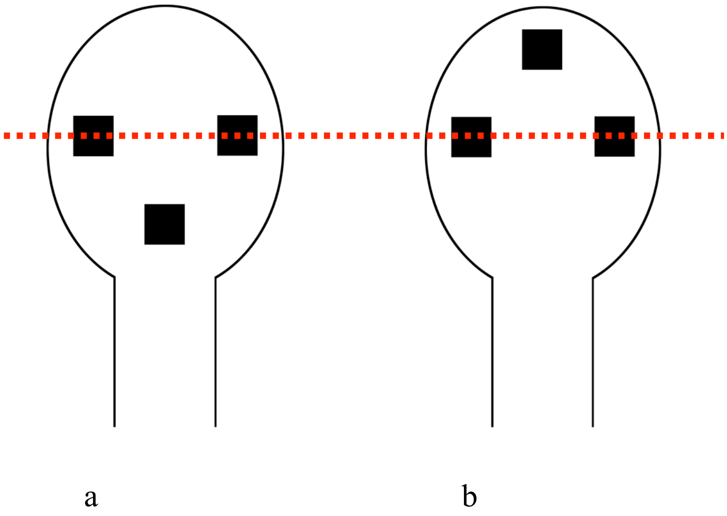


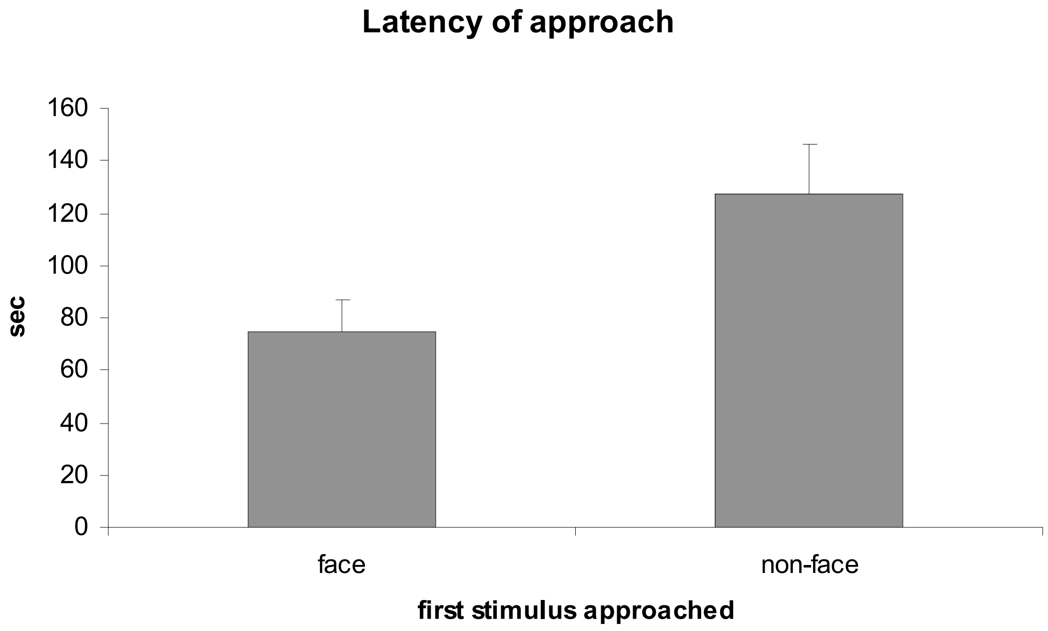
Figure 31
Representation of the two stimuli used in Experiment 3. Stimulus a) represents a bottom heavy face-like configuration, whereas stimulus b) is a top-heavy non-face-like configuration. Both stimuli are equally symmetrical along the vertical axis. The red dotted line was not present on original stimuli, and was here added on the purpose of illustrating that the two blobs representing the upper features of the face-like stimulus and the lower features of the non-face-like one occupied exactly the same position in the two stimuli.

### ***Results***

The number of chicks that approached the face-like configuration when leaving the centre of the apparatus for the first time during the test was not significantly different from the number of chicks that approached the non-face-like configuration first ($\chi^2_1 = 0.364$; $p = 0.546$; 20 chicks approached the face, 24 the non-face).

In line with this evidence, also the proportion of time spent near the face-like stimulus for the whole length of the test did not differ significantly from chance level ($t_{43} = -1.316$; $p = 0.195$).

As regards the latency to approach one stimulus when leaving the centre of the apparatus for the first time during the test, a significant effect of the first stimulus approached emerged. In fact, chicks approaching the face-like stimulus were significantly quicker than chicks approaching the non-face-like stimulus first ($t_{42} = -2.178$; $p = 0.028$). See Graph 3



Graph 3

Mean latency of first approach in Experiment 3, for chicks approaching the face-like stimulus (left hand side column) and for chicks approaching the non-face-like one (right hand side column). Group means (in seconds) with SEM are shown.

## Discussion

Results of the present experiment confirmed the results obtained in Experiment 1. In fact, in the presence of a face-like configuration, even if a bottom-heavy one, chicks seemed to prefer that configuration over a top-heavy non-face-like stimulus. However, results obtained in Experiment 3 differed from those of Experiment 1 in the dependent variables that revealed the preference expressed by chicks. In fact, in Experiment 1 chicks preference for the face like stimulus emerged as regards the standard dependent variables measured in this task to reveal social-preferences (namely the first stimulus approached and the ratio of time spent near the two stimuli). On the contrary, in Experiment 3, chicks' preference for the face-like stimulus emerged as a shorter latency to approach the face-like stimulus[47].

Possible explanations of such discrepancy between the results of Experiments 1 and 3 could be that either the complete expression of the preference for faces requires for the face-like configuration to be top-heavy (as in Experiment 1 but not in Experiment 3), or that in the present experiment chicks' preference for faces was contrasted with that for top-heavy configurations, and could be weakened by this contrast. However, both these explanations are not completely convincing: in fact previous experiments did not reveal any direct (Experiment 2) or indirect (Experiment 1) evidence of the presence of an up-down bias in chicks.

A further possibility is that the results of the present experiment actually reflected the presence of a weaker preference for the face-like stimulus with respect to Experiment 1, and this in turn could be due to a peculiarity in the experimental stimuli used. In fact, both the face-like and the non-face-like stimuli used in the present experiment were identical as regards the "eye-region", i.e. the position of the two blobs representing the "eyes" of the face stimulus was identical to the position of the corresponding blobs in the other stimulus. It is likely that the eye region plays a major role in determining preferences for face-like configurations in chicks, more than other "face traits" do (consistent with other evidence available in the literature on humans and animal species, e.g. Easterbrook, Kisilevsky, Hains and Muir, 1999; Farroni, Johnson, Menon, Zulia, Faraguna and Csibra 2005; Keating and Keating, 1982; Kendrick, 1991; Kendrick, Atkins, Hinton, Broad, Fabre-Nys and Keverne, 1995; Myowa-Yamakoshi and Tomonaga, 2001b; Tate, Fischer,

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[47] Latency of first approach is a dependent variable often sensitive to fear reactions elicited as part of anti-predatory responses (see for example Rosa Salva, Regolin and Vallortigara, 2007).

Leigh and Kendrick, 2006; Turati, Valenza, Leo and Simion, 2005). This could explain why the preference for a face-like configuration is weakened when this configuration is confronted with a non-face-like stimulus that is identical to the face-like one with regard to the “eye region”.

## Experiment 4

The aim of this experiment was to confirm the finding, that emerged from Experiments 1 and 3, that chicks' preference for schematic faces is maintained even when the role of the up-down bias is controlled for. We especially wanted to check whether it was possible to confirm the evidence of a preference for face-like stimuli when such a preference is put in direct conflict with the hypothetical influence of the up-down bias (i.e. to confirm that chicks prefer a bottom-heavy face-like stimulus with respect to a top-heavy non-face-like one). In fact, in Experiment 3 we obtained some evidence of a preference for a bottom-heavy face-like configuration with respect to a top-heavy, but non-face-like one. However, such evidence was obtained for a dependent variable different from the dependent variables that were sensitive to the preference for the face-like stimulus in Experiment 1, namely the latency of first approach. We thus decided to try to extend this result to one of the dependent variables that resulted sensitive to the preference for the face-like stimulus in Experiment 1, by increasing the effectiveness of our stimuli in eliciting a preference for faces.

We wanted to do so by investigating the role of the "eye region" of stimuli in determining preferences for faces. Our hypothesis was that, by using a pair of stimuli that (unlike in Experiment 3 see Figure 31, a and b) were not identical in the "eye region" - being thus also more similar to the original configurations used by Turati, Simion, Milani and Umiltà (2002) - the preference for the face-like configuration would be extended to some other dependent variables sensitive to social preferences (i.e. the first stimulus approached and/or the ratio of time spent near the two stimuli). For a reproduction of the stimuli used in Experiment 4, see Figure 32, a and b.

Two kinds of evidence were in favour of such a hypothesis. First of all, data are there in the literature suggesting a fundamental role of eyes in determining responses to faces (see the "Introduction" and the "Discussion of Experiment 3"). Moreover, in the present experiment an increased perceptual difference between the two test stimuli could facilitate the independent processing and differentiation of the face-like stimulus with respect to the non-face-like one. Thus, according to Morton and Johnson's (1991) hypothesis, the configurations used in the present experiment could be more likely to produce a significant preference for the bottom-heavy face-like stimulus. On the other hand, a further aim of the present experiment was also to test stimuli in which the top-heaviness and bottom-heaviness were more pronounced than in Experiment 3. As a consequence, the up-down bias theory (Turati, Simion, Milani and Umiltà, 2002) would predict that the pair of stimuli employed in Experiment 4 should be more effective in eliciting a preference for the top-heavy non-face-like configuration than those of the previous experiment.

### *Subjects*

Subjects were 58 (28 male and 30 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

The test stimuli used in Experiment 4 differed from those of previous experiments in the position of the three square black blobs. Similarly to Experiment 3, stimuli consisted of one top-heavy non-face-like configuration and one bottom-heavy face-like one, but in the new pair of stimuli, the two blobs representing the "eyes" of the face-like configuration were not placed at the same height as the corresponding blobs in the non-face-like configuration. In fact, the two blobs representing the eyes of the face-like stimulus were in a relatively lower position within the face outline (i.e. they were misaligned, see Figure 32, a and b). As a consequence, this new pair of stimuli was more similar to the original configurations used by Turati and her colleagues (2002), and was used in order to obtain stimuli which could possibly be more powerful in eliciting a preference for one of the two configurations with respect to those used in the previous experiment (see above).

With the stimuli employed in Experiment 4 we thus aimed to directly contrast the predictions advanced by the up-down bias theory (Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; Turati, Simion, Milani and Umiltà, 2002) and the CONSPEC-CONLERN model (Morton and Johnson, 1991; Johnson, 2005), as described for Experiment 3, but in a more effective fashion. According to the up-down bias theory a preference for the top-heavy but non-face-like stimulus should be evident in the present experiment, and should be more pronounced than in Experiment 3 (due to the fact that the top-heaviness and bottom-heaviness of the two stimuli are more evident). However, the opposite prediction is advanced by the CONSPEC-CONLERN model (see above).

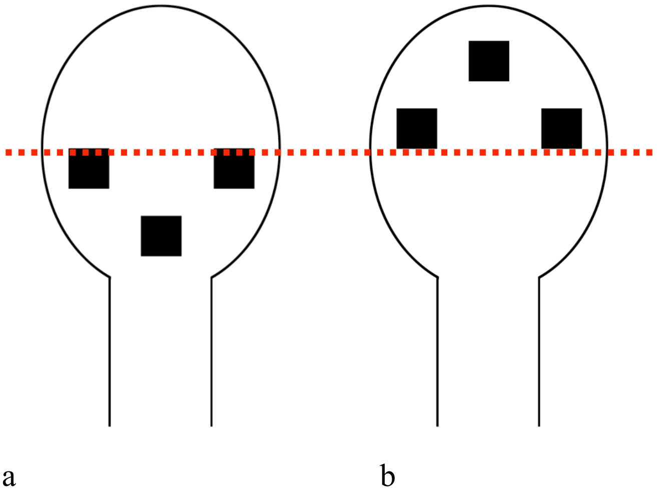
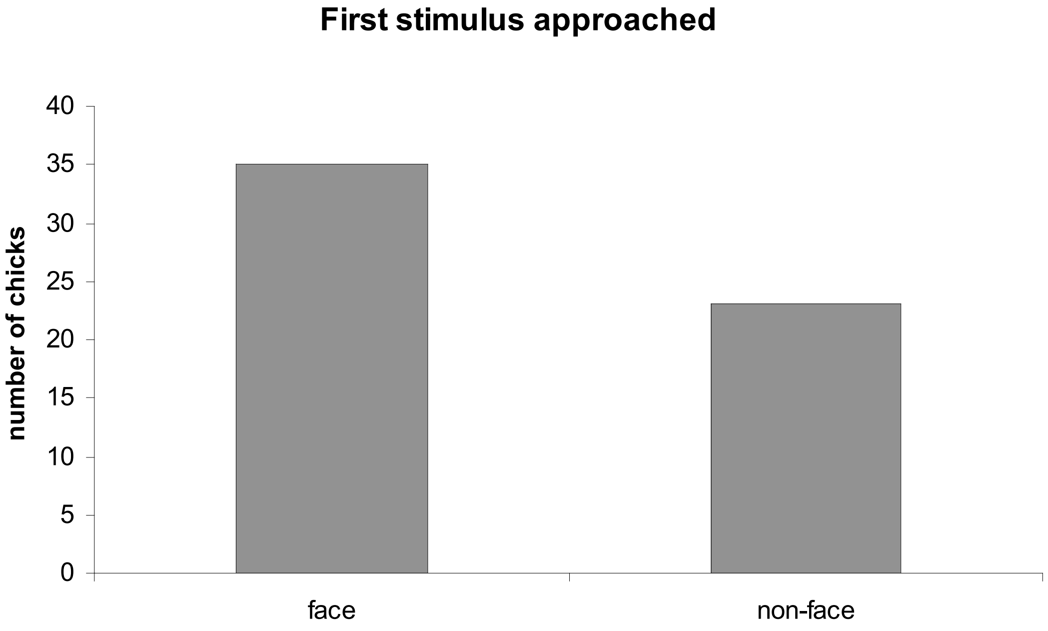


Figure 32
Representation of the two stimuli used in Experiment 4. Stimulus a) represents a bottom heavy face-like configuration, whereas stimulus b) is a top-heavy non-face-like configuration. Both stimuli are equally symmetrical along the vertical axis. The red dotted line was not present on original stimuli, and was here added on the purpose of illustrating that the two blobs representing the upper features of the face-like stimulus and the lower features of the non-face-like one were not aligned in the two stimuli.

### *Results*

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the face-like stimulus first, was not significantly different from the number of chicks that approached the non-face-like configuration first ($\chi^2{}_1$= 2.483; p = 0.115; 35 chicks approached the face, 23 the non-face), though there was a clear trend towards a preference for the face-like stimulus. See Graph 4.



Graph 4

Number of chicks approaching the face-like (left hand side) versus the non-face-like configuration (right hand side) as first stimulus during the test in Experiment 4.

In line with this trend, the proportion of time spent near the face-like stimulus for the whole length of the test was significantly different from chance level ($t_{57} = 2.089$; $p = 0.041$; MEAN = 60.581%, SEM = 5.066): chicks spent more time near the face-like configuration.

Finally, as regards the latency to approach one stimulus for the first time during the test, no significant effect of the first stimulus approached was observed ($t_{56} = 1.858$; $p = 0.068$). This meant that chicks were not significantly quicker when approaching the top-heavy over the bottom-heavy stimulus.

### *Discussion*

The results of Experiment 4 confirmed and extended those of Experiments 1 and 3. In fact, chicks tested in Experiment 4 preferred a face-like bottom-heavy stimulus over a non-face-like top-heavy one. The preference observed in Experiment 4 in favour of the face-like stimulus was evident in one of the traditional dependent variables used to measure social preferences in this task, i.e. the ratio of time spent near the face-like stimulus. Thus, results obtained in Experiment 4 reflected those of Experiment 1 more strictly than results of

Experiment 3 did. Moreover, the preference for spending more time near the face-like stimulus was observed using a pair of stimuli that, according to the up-down bias hypothesis, should be particularly effective in eliciting a preference for the non-face-like top-heavy stimulus (see above).

However, the results of Experiment 4 differed from those of Experiment 1 in that no significant preference for the face-like stimulus emerged for the dependent variable “first stimulus approached” (though there was a clear trend in that direction). Again, a possible explanation could be that, in the present experiment, the preference for faces was partially counterbalanced by a preference for top-heavy stimuli. Results obtained in Experiment 2 render, however, this explanation quite unlikely, due to the absence of evidence of a preference for top-heavy stimuli when no face-like configuration is there.

The present result, being consistent with that of Experiment 1, is particularly remarkable in the light of the fact that it reflects the presence of a stronger preference for faces when the test stimuli used differed in their eye-region (as in the present experiment), with respect to a situation in which both test stimuli were identical in eye-regions (as in Experiment 3). This result can be explained in the light of a crucial role of the stimuli eye region in eliciting preferences for faces (see discussion of Experiment 3).

## General discussion of Experiments 1-4

The results obtained in Experiments 1-4 demonstrate that domestic chicks, visually inexperienced with respect to faces, spontaneously prefer schematic stimuli presenting a face-like arrangement of internal features, even when the role of the up-down bias is controlled for. This finding is relevant from several points of view.

First of all, this is, to the best of our knowledge, the first demonstration that chicks are sensitive to *facedness* when this property is embedded into a highly schematic stimulus, such as those usually employed for testing face-preferences in human babies. Our results imply that further studies could make use of this peculiarity of the social behaviour of chicks to compare the results obtained in human newborns with respect to chicks' responses to similar stimuli, exploiting the many possibilities given by this flexible animal model for the investigation of the neural bases of the predisposition for faces.

Moreover, the results obtained seem to be in agreement with the existence, put forward by Morton and Johnson (1991), of an innate representation (CONSPEC) shared among vertebrates that directs the animals' attention toward stimuli whose internal features are arranged according to a triangular face-like configuration. The presence of such a representation in domestic chicks is not completely unexpected. It was already known that chicks prefer to approach naturalistic stimuli that resemble a hen (such as a stuffed hen), and that the presence of the inner features of the hen's head and face arranged according to their natural structure (i.e. maintaining their reciprocal spatial positions) was crucial for eliciting that preference (Johnson, Bolhuis and Horn, 1985; Johnson and Horn, 1988). Data present in the literature also suggested that the representation of a social object that underlies this preference in chicks could be quite generic and broad (probably, broad enough to be activated when schematic stimuli are employed) (Johnson and Horn, 1988). The preference expressed by chicks in previous studies was so broad, in fact, as to be even not species-specific: naïve chicks approached a mammal and a potential predator, such as a polecat, to the same degree as they approached a hen (Johnson and Horn, 1988). Similarly, visually-naïve chicks did not show any preference between a point-light-display representing the motion pattern of a walking hen or that of a cat (Vallortigara, Regolin and Marconato, 2005). The species-specificity or non-species-specificity of chicks' face preferences will be further investigated in Experiment 5.

On the other hand, our results are not consistent with the up-down bias theory that claims that the preference for face-like configurations in human newborns would emerge only as a secondary effect of a non-specific bias favouring top-heavy configurations. Contrary to the results obtained with human newborns by Turati, Simion, Milani and Umiltà (2002), chicks seem to prefer face-like stimuli even when they are confronted to other top-heavy configurations (Experiment 1), or when the face-like stimulus itself is a bottom-heavy configuration that is confronted with a top-heavy non-face-like stimulus (Experiments 3 and 4). On the other hand, non-face-like top-heavy configurations do not elicit a spontaneous preference *per se* (Experiment 2). Admitting that non significant results should be considered with caution, it is all the same possible to argue that, if any preference for top-heavy configurations would be present in chicks, this preference should definitely be weaker than that expressed by chicks for face-like stimuli and as such less effective than the up-down bias observed in newborns. In fact, in chicks any hypothetical up-down bias does not play a crucial role in determining the preference for faces, and it does not seem to be strong enough to negate such a preference.

Let us consider some possible explanations for the presence in chicks of a weaker (with respect to human newborns), or absent, up-down bias. A first possibility is that the up-down bias, in order to emerge, would depend to the presence of a certain degree of visual experience with faces (which was completely prevented in the chicks, which were tested when visually *naïve* with respect to faces' inner structure). For obvious reasons, such a striking control of visual experience cannot be obtained in experiments with human infants (and this is in fact one of the reasons of the interest in the use of animal model systems).

Another possible explanation was suggested to us by Francesca Simion (*personal communication*, 2008), who noticed that the experimental procedure used in the present work (unlike that used with human newborns by Simion, Valenza, Macchi Cassia, Turati and Umiltà, 2002; and Turati, Simion, Milani and Umiltà, 2002) did not control for the presentation of the stimuli in terms of upper versus lower visual-hemi-field. In fact, chicks were completely free to move and to visually explore stimuli during the test. It should be noted, however, that this explanation would apply mainly to the null results obtained in Experiment 2 because Experiments 1, 3 and 4 provided direct evidence of a preference opposite to that predicted on the basis of the up-down bias theory. Moreover, if the up-down bias were to be effective in determining newborns' behaviour only under such extremely controlled visual conditions (i.e. only if the stimulation provided to each part of the visual field would be rigidly determined), the potential role and relevance of such a bias in an ecological situation would appear questionable. An organism is likely to need and evolve mechanisms enabling it to preferentially pay attention to social partners within its natural environment and natural free viewing conditions.

A further explanation for the differences observed here in chicks with respect to human newborns could be that mechanisms underlying face preferences evolved by the two species are different. This is not unreasonable, of course, considering the phylogenetic distance between the two species. Chicks could possess a more specific face detection mechanism (i.e. a relatively "detailed" representation of the appearance of a face, as defined by its triangular arrangement of inner features) than human newborns' (which may simply possess a general preference for top-heavy stimuli). It can be hypothesized that the offspring of a precocial species ready to imprint on the first salient object encountered, such as a domestic chick, could be in need of the ability to accurately discriminate biological objects with respect to inanimate ones. In fact, the consequences of a false positive response (i.e. responding to an inanimate object by mistaking it for a face) would be extremely disadvantageous for a young animal that may imprint on an inanimate feature of the surrounding environment, being as a consequence separated from the mother hen. On the contrary, for a newborn human the same false positive response (i.e. considering one inanimate top-heavy object as if it was a face) would only imply the loss of one opportunity of social intercourse with the caretaker. Moreover, it seems unlikely that this kind of false alarm would be too frequent in newborn humans due to the further constraints imposed by their sensitivity to the contrast polarity and shadow pattern typical of a face under natural illumination conditions (Farroni, Johnson, Menon, Zulian, Faraguna and Csibra, 2005). It remains to be seen, however, whether similar phenomena will be observed in chicks as well. This issue is investigated in Experiments 6-11 that will test the role of contrast polarity by investigating the effects of contrast negation on chicks' face preferences. Spatial frequencies composing stimuli are another potentially relevant property identified in studies on human newborns' face preferences (Kleiner, 1987; Valenza, Simion, Macchi Cassia and Umilità, 1996). The role of this perceptual property of stimuli in eliciting chicks' face preferences, will be investigated in Experiment 5. Experiment 5 will, moreover, extend the amount of data available on the parallelisms observed between domestic chicks' and human newborns' face preferences, by directly comparing data available for domestic chicks and human newborns tested with the same stimuli and most highly comparable procedures.

Another interesting finding of the present experiments relates to the importance of features present within the area on the stimuli corresponding to the eyes in determining chicks' preferences (Experiments 3 and 4). This is consistent with other evidence present in the literature in favour of the hypothesis that eyes play a dominant role in determining face preferences in human babies and animals (see Discussion of Experiment 3; see also Easterbrook, Kisilevsky, Hains and Muir, 1999; Kendrick, 1991; Kendrick, Atkins, Hinton, Broad, Fabre-Nys and Keverne, 1995; Myowa-Yamakoshi and Tomonaga, 2001b; Turati, Valenza, Leo and Simion, 2005). It has to be noted that evidence in favour of the crucial importance of eyes could fit well with either the up-down bias hypothesis (eyes are the most important feature of the face because they are placed in its upper part) or the CONSPEC hypothesis (eyes are crucial due to their importance for social communication, Farroni, Johnson, Menon, Zulian, Faraguna and Csibra, 2005). The comparison between the results obtained in Experiments 3 and 4 gives us the possibility to speculate that the predominant role of eyes in face preferences of chicks could be difficult to account for in terms of the up-down bias hypothesis. In fact, we found evidence suggesting that there is a major role of eyes in determining face-preferences in a context in which the preferred, face-like, stimulus presented "eyes" in its lower part.

It has long been debated as to whether newborns' face preferences, and in general face perception abilities, are served by specific mechanisms (and the role of experience in determining such mechanisms is still debated too, see "Introduction"). Results obtained so far in the present work seem to support the presence of a face-specific mechanism underlying innate preferences expressed by newborn domestic chicks. Even more strikingly, this domain-specific mechanism does not require any prior experience of the inner structure of a face in order to emerge. The presence of an inborn representation of face structure demonstrated here could constitute the basis for an innate conspecific-detector device, possibly shared among different classes of vertebrates. Very likely, this mechanism could actually act as part of a general social -or biological- object detector (for similar evidence of an innate ‘life detector device’ in chicks see also the paragraph “Presence of an unlearned representation of social objects in chicks”; Vallortigara, Regolin and Marconato, 2005; Vallortigara and Regolin, 2006).

## Experiment 5

Converging evidence from different species indicates that newborn vertebrates, including humans and domestic chicks, have visual predispositions to attend to the head region of conspecifics (e.g. Johnson and Horn, 1988; Morton and Johnson, 1991; Sugita, 2008). Results obtained in Experiments 1-4 in visually deprived chicks confirmed this evidence as regards chicks' preferences for schematic face-like stimuli (similar to those used in studies with human newborns). Stimuli of Experiments 1-4 were balanced in terms of the up-down bias, allowing us to rule out such a bias as a causal factor in chicks' face preferences. Stimuli used in Experiments 1-4 were also controlled in terms of properties such as vertical symmetry (in fact configurations used in each experiment were either both symmetrical or both asymmetrical on the vertical axis) and presence of a recognizable figure structure (both configurations used in each experiment shared the same outline).

In the present experiment we thus decided to further investigate the presence of convergencies between evidence obtained in domestic chicks and human newborn babies, by directly comparing data obtained in newborn babies with data obtained in visually naïve domestic chicks, tested with identical stimuli and comparable procedures. Moreover, a further aim of the present experiment was to test the role of another perceptual property considered potentially relevant in developmental studies on face preferences, namely spatial frequencies composing stimuli. In the developmental literature it has been widely debated whether face preferences of newborn babies could be simply due to the fact that faces happen to contain the range of spatial frequencies most visible to newborns (Acerra, Burnod and de Schonen, 2002; Kleiner, 1987; Morton and Johnson, 1991; Valenza, Simion, Macchi Cassia and Umiltà, 1996). The use of stimuli that exactly match spatial frequencies between face-stimuli and control-stimuli, comparing faces to frequency matched visual noise, is already a common standard in works investigating neural correlates of face perception in newborn babies (Blasi, Fox, Everdell, Volein, Tucker, Csibra, Gibson, Hebden, Johnson and Ellwell, 2007; Csibra, Henty, Volein, Ellwell, Tucker, Meek and Johnson, 2004). However, this approach had not yet been systematically applied to the investigation of behavioural preferences in newborn babies. In order to bridge this gap between behavioural data and neuroimaging or ERP data, in a previous study we tested newborn babies' preferences for photographic images of faces with respect to visually matched noise stimuli containing the same spatial frequencies as the face stimuli. In this study we obtained clear evidence of a preference for observing the face stimulus in newborn babies.

In Experiment 5, we thus decided to run a truly comparative study by testing chicks' preferences for the same stimuli that we previously employed in newborns (Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, under revision). In fact, one of the most common criticisms of the work supporting domain-relevant face biases in human newborns is that in most studies subjects were already a few hours old when tested. Criticisms of the data from human newborns can be addressed by testing newly hatched visually-deprived chicks whose preference for visual stimuli can be assessed prior to any other visual experience with faces. In the present experiment, for the first time, we test the prediction that visually deprived newly hatched chicks and human newborns would demonstrate similar preferences for face stimuli over spatial frequency matched structured noise.

Moreover, the pair of stimuli used in Experiment 5, allowed us to test also the species-specificity of the face-preference displayed by chicks: in fact, the face-stimulus employed in the present experiment consisted in a photographic image of a human face. Previous evidence present in the literature suggests that chicks' social preferences are based on a representation of a social object so broad as to be non-species-specific (e.g see Johnson and Horn, 1988). Thus, chicks' face preferences should extend also to faces of other vertebrate species. To the best of our knowledge, this is the first experiment that directly tests this prediction in visually naïve chicks.

### *Subjects*

Subjects were 40 (20 male and 20 female) domestic chicks (*Gallus gallus domesticus*).

***Rearing conditions***

Chicks were reared exactly as described in the "General materials and methods" paragraph, but in the absence of any imprinting object.

***Test stimuli***

The stimuli were a pair of images employed in the human newborn experiment that we previously conducted (Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, under revision), which had been also previously used in two human neuroimaging studies (Blasi, Fox, Everdell, Volein, Tucker, Csibra, Gibson, Hebden, Johnson and Ellwell, 2007; Csibra, Henty, Volein, Ellwell, Tucker, Meek and Johnson, 2004). Stimuli consisted in a full colour image of a female human face (face stimulus) and a scrambled version of the same image (noise stimulus) artificially constructed with the same spatial frequencies and colour as the corresponding face (see Figure 33) (see Blasi, Fox, Everdell, Volein, Tucker, Csibra, Gibson, Hebden, Johnson and Ellwell, 2007 for details). Stimuli were 9 cm high x 9 cm large.

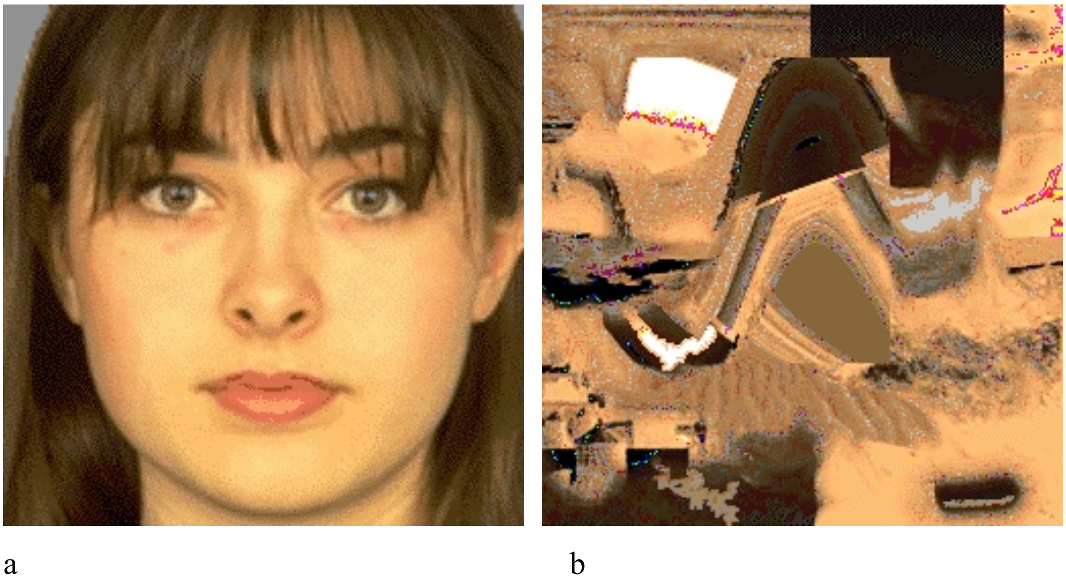


Figure 33

Representation of the stimuli used Experiment 5. Stimulus a) is a colour photographic image of a human female face; stimulus b) is a visually matched noise stimulus artificially constructed in order to contain the same spatial frequencies, colour distribution and luminance of the face stimulus.

Using this pair of stimuli we were thus able to simultaneously test the role of spatial frequencies composing stimuli, and to parallel previous evidence obtained in newborns. As regards spatial frequencies, if chicks' face preferences were due the spatial frequencies composing stimuli, no preference for the face stimulus should be evident in the present experiment (Kleiner, 1987; Morton and Johnson, 1991, see the paragraph "Role of spatial frequencies composing stimuli"). On the contrary, if chicks' preferences would be directed by a CONSPEC-like device, chicks should prefer the stimulus presenting the overall configuration of a face. Moreover, if, as suggested by previous evidence available in the literature (e.g see Johnson and Horn, 1988), chicks' face preferences can extend also to faces of other vertebrate species, a preference for the stimulus representing a human face should be observed in the present experiment.

### *Procedure*

Chicks were tested exactly as described in the "General materials and methods" paragraph, with the only exception of an additional dependent variable that was collected in Experiment 5 only. In fact, in order, to allow a more direct comparison with newborns' data, chicks' head orienting responses were also recorded. This measure was collected in order to correspond to one of the traditional dependent variables measured in newborn babies, i.e. number of gaze orienting responses toward the two stimuli.

A head orienting response was defined as a discrete head turning movement, which leads the chick to fixate one of the two stimuli within its binocular central visual field. Operationally, this meant that an orienting response was scored whenever the chick directed the tip of its bill toward one of the two stimuli. In order to record an orienting response the following criteria were used:

- the chick had to be still when the orienting response was performed (this mainly led to the exclusion of responses performed while the chick was walking);
- the starting-orientation of the head, before the beginning of the response, had to be equidistant from the two stimuli (i.e. none of the two stimuli had to be

already fixated within the frontal binocular visual field before the beginning of the response);

- pecking responses which also induced a change in head orientation were not considered orienting responses (i.e. head movements incidentally performed while the chick was pecking at an object in the environment, most often its own feet, were not considered).

***Data analysis***

To represent the proportion of head orienting responses performed toward the face stimulus, an index was calculated from number of head orienting responses performed toward the two stimuli using the formula:

$$\left(\text{Orienting responses toward face} \,/\, \text{Orienting responses toward face} + \text{Orienting responses toward noise stimulus}\right) \times 100$$

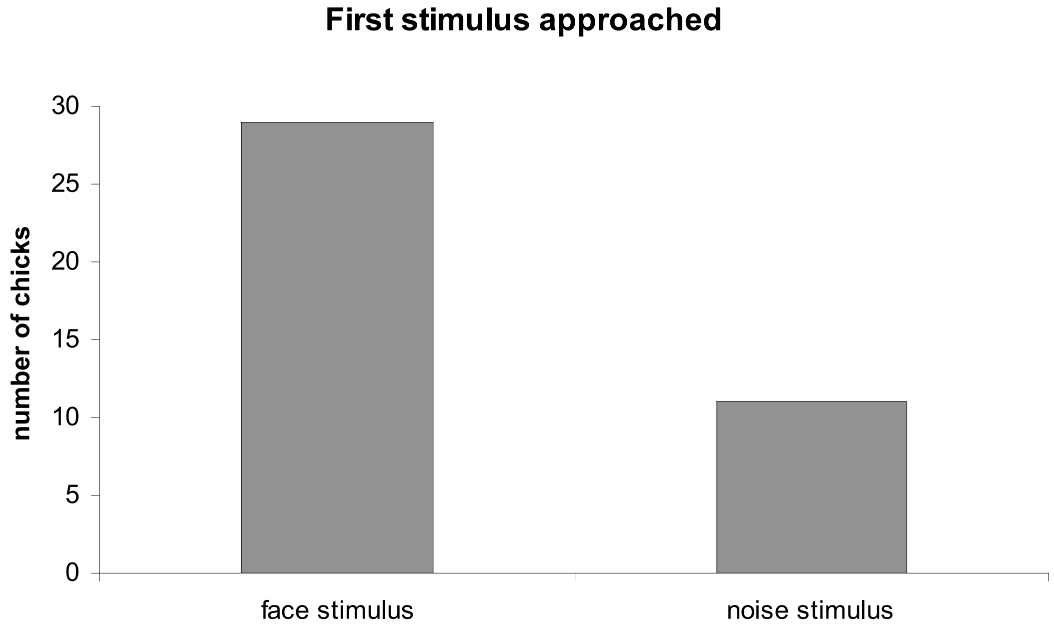
This index was analyzed exactly as described for the ratio of time spent near the two stimuli: significant departures from chance level (50), which indicated a preference for the face (> 50) or noise stimulus (< 50), were estimated by one-sample two-tailed *t*-test.

In addition to the standard data analysis conducted for all experiments, in Experiment 5 we also decided to directly compare data obtained by our chicks and by the newborn babies tested with the same stimuli and comparable procedures in the previous experiment we conducted (Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, under revision). As regards the dependent variables representing the proportion of head orienting responses toward the face stimulus and the ratio of time spent near the face stimulus, data collected in chicks of Experiment 5 were thus compared, via independent-sample t-tests, with the data of newborn babies for the corresponding dependent variables (i.e. respectively the proportion of gaze orienting responses toward the face stimulus performed by newborns and the ratio of total fixation time spent by newborns looking at the face stimulus).

Newborns' data employed for this comparison with chicks, were collected on a sample of 13 babies, using a paired visual preference task with an infant control procedure. In this task, two stimuli (a photographic image of a human face and a visually matched noise stimulus, the same stimuli employed with chicks in Experiment 5, see above) were simultaneously presented at the two sides of a screen. Once the newborn was seated in front of the screen, as soon as she/he fixated the centre of the screen, the experimenter (who watched the newborn's eyes via a video monitor system) initiated a trial and presented the stimuli on the screen. The stimuli remained on for as long as the infant fixated one of them (infant control procedure). When the infants shifted their gaze away from the display for more than 10 sec, the experimenter removed the stimuli and presented the next trial. In the second trial the location of the stimuli was reversed. Videotapes of the baby's eye movements throughout the trial were subsequently analyzed by two coders blind as to the location of noise and face stimuli. The coders recorded, separately for each stimulus and each trial, the number of orienting responses and the total fixation time. Dependent variables considered were the number of orienting responses (i.e. fixations) directed at the two stimuli and the total amount of time spent fixating each one of the two stimuli for the whole length of the test. To represent the proportion of gaze orienting responses performed toward the face stimulus and the ratio of total fixation time spent looking at the same stimulus, an index was calculated from each dependent variable, using an analogous formula to that described for chicks (see above). For a detailed description of the methods and procedures used to collect these measures in newborns see Rosa Salva, Farroni, Regolin, Vallortigara and Johnson (under revision).

### *Results*

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, a significantly greater number of chicks approached the face stimulus first with respect to the number of chicks that approached the noise stimulus first ($\chi^2_1 = 8.100$, $p = 0.004$; 29 chicks approached the face and 11 approached the noise stimulus). See Graph 5.



Graph 5

Number of chicks approaching the face stimulus (left hand side) versus the noise stimulus (right hand side) as first stimulus during the test in Experiment 5.

Moreover, the percentage of discrete head orienting responses performed by the chicks toward the face stimulus during the whole length of the test was significantly higher than what expected by chance level ($t_{39} = 2.999$, $p = 0.005$; Mean = 58.594%, SEM = 2.865%). This meant that chicks oriented their head significantly more times to look toward the face stimulus than toward the noise stimulus.

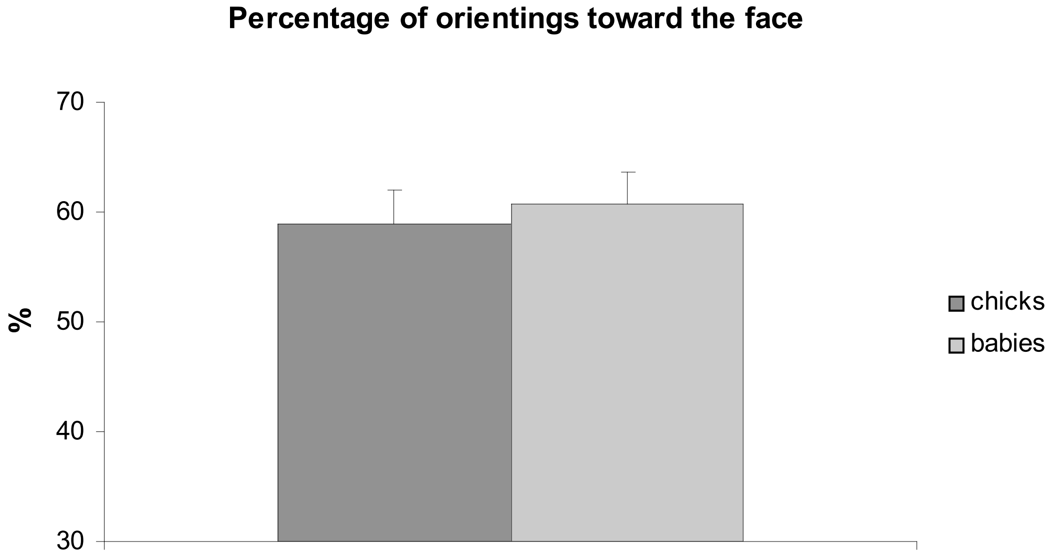
In line with the evidence described above, also the ratio of time spent near the face stimulus was significantly higher than expected by chance level ($t_{39} = 3.821$, $p = 0.000$; Mean = 71.135%, SEM = 5.532%), meaning that chicks spent significantly more time near the face stimulus than near the noise stimulus.

However, as regards the latency to approach one stimulus for the first time during the test, no significant effect of the first stimulus approached was observed ($t_{38} = -.470$; $p = 0.641$). This meant that chicks were not significantly quicker when approaching the face over the noise stimulus.

Thus, the analysis of all dependent variables with the only exception of the latency to approach, demonstrated the presence of a preference for approaching, looking and staying near the face stimulus with respect to the noise stimulus.

We also compared data obtained in chicks with data previously obtained in newborn babies tested with the same stimuli (Rosa Salva, Farroni, Regolin, Vallortigara and Johnson, under revision).

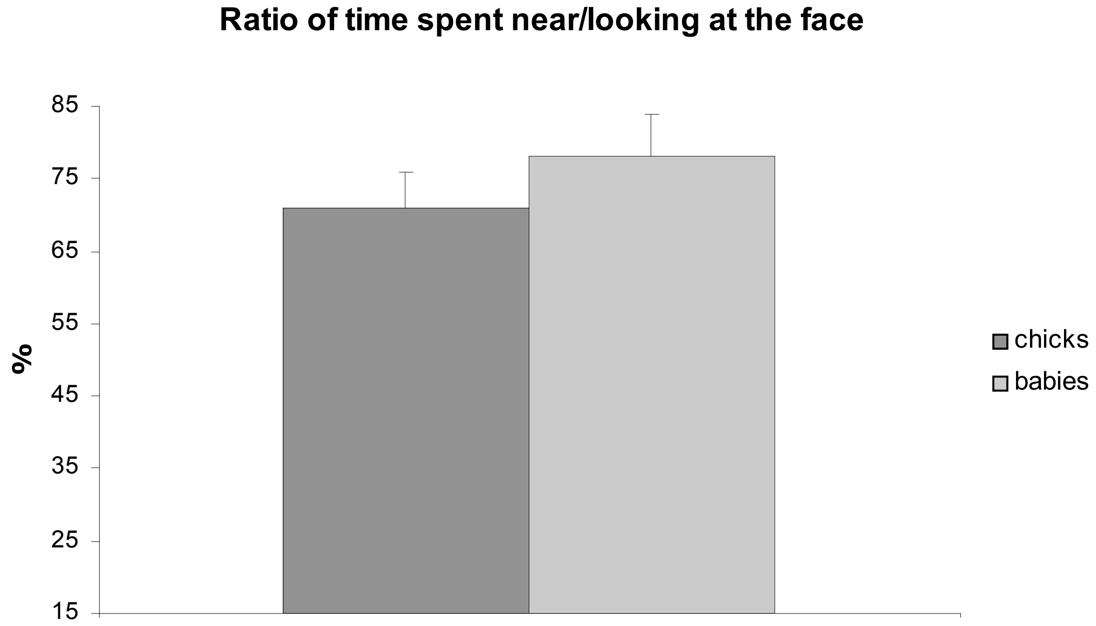
In particular, the percentage of head orienting responses performed by chicks toward the two stimuli was compared with the percentage of gaze orienting responses performed by newborn babies. This comparison resulted not significant ($t_{51} = -0.422$, $p = 0.675$). See Graph 6.



Graph 6

Mean percentage of head orienting responses performed toward the face stimulus by domestic chicks tested in Experiment 5 (darker column) and mean percentage of gaze orienting responses performed toward the face stimulus by the newborn babies tested by Rosa Salva, Farroni, Regolin, Vallortigara and Johnson (under revision) (lighter column). Group means with SEM are shown.

Similarly, we compared the ratio of time that chicks spent near the face stimulus with the ratio of time that newborn babies spent looking at the same stimulus, and also this comparison resulted not significant ($t_{51} = -0.966$, $p = 0.340$). See Graph 7. Thus, the degree of preference for the face stimulus observed for the two above mentioned dependent variables was identical in chicks and newborn babies.



Graph 7

Mean proportion of time spent near the face stimulus by domestic chicks tested in Experiment 5 (darker column) and mean proportion of time spent looking at the face stimulus by the newborn babies tested by Rosa Salva, Farroni, Regolin, Vallortigara and Johnson (under revision) (lighter column). Group means with SEM are shown.

### *Discussion*

Data obtained in Experiment 5 demonstrated that visually naïve domestic chicks have a spontaneous preference to approach, stay near and orient their head toward a face stimulus, when this stimulus is compared with a visually matched noise stimulus containing the same spatial frequencies as the face stimulus. Moreover, the degree of preference for the face stimulus was directly compared between visually naïve domestic chicks and human newborn babies. This comparison revealed that data obtained in the two species were undistinguishable.

These results are relevant from different points of view.

First of all, data obtained in Experiment 5, confirm and extend results emerged in Experiments 1-4, as regards chicks' spontaneous preferences for faces. In fact, in Experiment 5 chicks' preference for faces emerged using stimuli that differed from those employed in Experiments 1-4 in many aspects. It was thus possible to extend our knowledge of chicks' face preferences, demonstrating that such preferences can emerge also using photographic images of faces, instead of schematic face-like stimuli. This further increases the existing parallels between human infants' and domestic chicks' face preferences. Recent studies investigated human infants' face preferences using photographic images of human faces instead of schematic face-like stimuli (e.g. Macchi Cassia, Turati and Simion, 2004). It was thus important to demonstrate the possibility to effectively test chicks' preferences with this kind of stimuli.

Moreover, the stimuli used in Experiment 5 allowed us to test the presence of non-species-specific face preferences in domestic chicks (in fact the face stimulus used in Experiment 5 represented the photographic image of a human face). Face preferences are not species specific in domestic chickens. This result is in line with previous evidence showing that spontaneous social preferences of domestic chicks are not selective for the species the animal belongs to. For example, Johnson and Horn (1988) demonstrated that visually naïve chicks approached a stuffed hen to the same extent that they approached a stuffed polecat (a potential predator for this species). Similar evidence has also been obtained in studies investigating chicks' preference for point light displays representing the biological motion pattern typical of different animal species. The point light display representing the biological motion pattern of a walking hen was in fact equally preferred to that of a walking cat (Vallortigara, Regolin and Marconato, 2005). Similar evidence was also obtained for human newborn babies, that showed a preference for the biological motion pattern of a walking hen (Simion, Regolin and Bulf, 2008). This result suggests that the presence of non-species-specific social preferences could be a common trait shared by many vertebrate species. In line with this hypothesis is also a recent work conducted by Sugita (2008). This author demonstrated that, prior to visual experience with faces, monkeys do not show any preference for looking at monkey or human faces, nor are they better able to recognize individual monkey faces with respect to individual human faces. The evidence described above is thus in line with the presence of a very broad template for the detection of faces, available to newborn vertebrates prior to any experience with faces. The information conveyed by this innate representation of faces' structure would be extremely generic and so broad to be not sufficient to allow any initial preference for conspecific faces over faces of other species. This scenario fits very well with the presence of a CONSPEC-like mechanism, such as that theorized by Johnson (Morton and Johnson, 1991; Johnson, 2005). However, this does not exclude the possibility that experience-driven specialization mechanisms, such as those hypothesised by the "perceptual narrowing" account (Nelson, 2001), would direct the further development of face-processing devices in social vertebrate species, after the initial action of the CONSPEC-like predisposition to attend to face-like stimuli. This would, for example, explain why the "other species effect" or the "other race effect" in human beings are absent during the first months of life and appear only later in development (Pascalis, de Haan and Nelson, 2002). Moreover such effects seem to be highly influenced by visual experience with a certain kind of faces (Pascalis, Scott, Kelly, Shannon, Nicholson, Coleman and Nelson, 2005; Sangrigoli, Pallier, Argenti, Ventureyra and de Schonen, 2005). Finally, also some data obtained by Sugita (2008) are in favour of the presence of experience-driven specialization mechanisms: monkeys that were exposed either only to monkey faces or only to human faces developed a preference for the kind of faces to which they had been exposed, and lost the ability to process the other kind of faces.

Another crucial aspect in which stimuli used in Experiment 5 differed from stimuli used in Experiments 1-4 is the fact that, in Experiment 5, stimuli were controlled for the role of different low-level perceptual properties. In Experiments 1-4 configurations used were balanced in terms of properties such as structure, vertical symmetry and vertical asymmetry in the distribution of inner elements, whereas in Experiment 5 the face stimulus and the control noise stimulus were matched in terms of the component spatial frequencies, colour distribution and luminance. Thus, Experiment 5 allows us to rule out the role of another potentially relevant perceptual property, such as spatial frequencies composing stimuli, in chicks' face preferences. This result is relevant first of all because the role of spatial frequencies has been much debated in the developmental face-perception literature (see e.g Acerra, Burnod and de Schonen, 2002; Kleiner, 1987; Morton and Johnson, 1991; Valenza, Simion, Macchi Cassia and Umilità, 1996) and results and explicative factors seem to be still controversial (see e.g. the different interpretations provided by Valenza, Simion, Macchi Cassia and Umilità, 1996; Acerra, Burnod and de Schonen, 2002). Thus, the use of stimuli matched in terms of spatial frequencies is an important control in order to understand the origins and underlying mechanisms of face preferences. This procedure is already a common standard in studies investigating the neural correlates of face preferences (Blasi, Fox, Everdell, Volein, Tucker, Csibra, Gibson, Hebden, Johnson and Ellwell, 2007; Csibra Henty, Volein, Ellwell, Tucker, Meek and Johnson, 2004). However, up to the study conducted with newborn babies by Rosa Salva, Farroni, Regolin, Vallortigara and Johnson (under revision), this approach had not yet been systematically applied to the investigation of behavioural preferences in newborn human infants. The study by Rosa Salva, Farroni, Regolin, Vallortigara and Johnson (under revision), that obtained clear evidence of a preference for observing the face stimulus in newborn babies, contributed to bridge the gap between behavioural data and neuroimaging or ERP data in human infants. Results obtained in Experiment 5, create a direct parallel between human newborns and domestic chicks on this regard, constructing the basis for further future comparative studies investigating the neural substrates of face preferences in these two species.

Finally, one of the most interesting aspects of the results obtained in Experiment 5 is the direct comparison between data obtained in human newborns and visually deprived domestic chicks, tested with identical stimuli and similar procedures. In the present experiment assessed the claim that some vertebrate species have predispositions to attend to stimuli that resemble the faces of conspecifics. It has been claimed that faces have a “special” status in visual processing, due to their relevance in social life throughout evolution. From a developmental perspective, this means that newborn animals should be equipped with domain-relevant preferences (likely to engage attention on faces occurring in the natural environment), which are unlearned and mediated by phylogenetically ancient brain routes common to many vertebrates. We tested this hypothesis by investigating preferences displayed by newly hatched chicks, naïve with respect to faces, and comparing their preferences with those displayed by human newborns. Both species significantly preferred to approach faces (chicks) or to observe faces (chicks and human newborns) compared to the control stimuli. This result is remarkable for two reasons. First of all, the findings reduce the likelihood that face-preferences in human newborns are based on very rapid learning during the first hours. In fact, for practical and ethical reasons it is hard to test truly naive human newborns. However, chicks tested in the present study showed exactly the same preference as newborns, but in the absence of any prior visual experience with faces. The second striking aspect of the present results is the convergence between face preferences displayed by the newborns of two phylogenetically distant vertebrate species. The convergence of results between those two species, and some possible causal explanations of such, will be discussed in detail in the “Conclusions” paragraph.

## Experiment 6

The aim of the present experiment was to investigate the effect of contrast polarity reversal on chicks' face preferences. In Experiment 1 we successfully demonstrated a preference for a schematic face-like stimulus that presented the contrast polarity expected for a face (i.e. darker inner face features on a lighter face background). Recent data on human babies suggest that in newborns face preferences could be sensitive to the reversal of contrast polarity. In fact, human newborns' face preferences disappear when negative images of faces are used as stimuli (Farroni, Johnson, Menon, Zulia , Faraguna and Csibra, 2005), in line also with the limited ability that adults show for the recognition of faces when presented as photographic negatives (e.g. Gilad, Meng and Sinha, 2009). It has been suggested that such effect of the reversal of contrast polarity could be a further element in favour of the domain-specificity of human face preferences and face processing abilities. In fact, if the preferences displayed by newborns would be "face relevant" (i.e. evolved to be efficient in drawing infants' attention to faces in a natural environment), newborns should be sensitive to contrast polarity. By being sensitive to contrast polarity the visual system of a newborn baby could efficiently detect faces in a natural environment under natural (top-lit) illumination, by responding to the light-shadow pattern generated on faces by such conditions. This is due to the fact that the eye and mouth regions are recessed on a face and therefore appear to be darker than other parts of the face that are directly illuminated. Thus, infants should show no preference for face-like patterns where the elements within the face are lighter than the background, because those elements would indicate protrusions rather than recesses for their visual system and this is exactly what has been found (Farroni, Johnson, Menon, Zulia , Faraguna and Csibra, 2005).

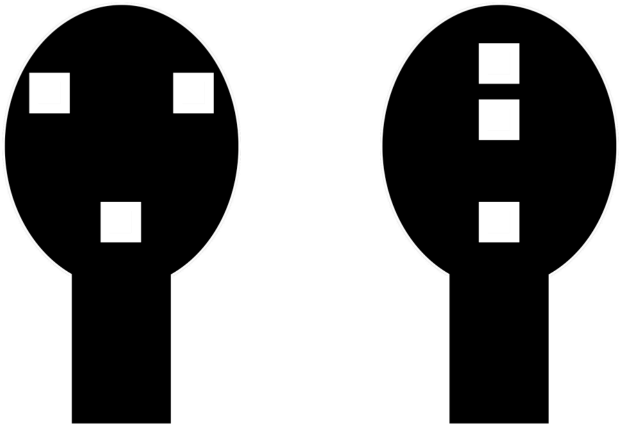
In the present experiment we thus decided to investigate this issue in chicks' face preferences, by testing their spontaneous choice for a negative version of the face-like stimulus used in Experiment 1, which was now composed of lighter face features on a darker background.

### *Subjects*

Subjects were 62 (31 male and 31 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

Test stimuli employed for Experiment 6 were identical to those used in Experiment 1, except that stimuli used in Experiment 6 presented a reversed contrast polarity with respect to Experiment 1. That is to say that, whereas in Experiment 1 the stimuli inner features were darker than the face background, in Experiment 6, stimuli inner features were lighter than the face background. Thus, in Experiment 1, but not in Experiment 6, the face-like stimulus presented the "correct" direction of contrast polarity expected for a face stimulus. See Figure 34.



a b

Figure 34

Representation of the stimuli used in Experiment 6. Stimulus a) represents a negative version of the top-heavy face-like stimulus used in Experiment 1, whereas stimulus b) represents a negative version of the top-heavy non-face-like stimulus used in Experiment 1.

Using this pair of stimuli we were able to test the effect of contrast reversal on chicks' face preferences. In fact, if contrast reversal abolishes chicks' face preferences, no preference for the face-like stimulus should be observed in the present experiment. On the contrary, if chicks preferences would not be sensitive to contrast reversal, a preference for the face-like stimulus should be observed, in line with results obtained in Experiment 1.

***Results***

The number of chicks that approached the face-like configuration when leaving the centre of the apparatus for the first time during the test, was not significantly different from the number of chicks that approached the non-face-like configuration first ($\chi^2_1 = 0.050$; $p = 0.823$; 39 chicks approached the face, 41 the non-face).

Moreover, in line with this evidence, also the proportion of time spent near the face-like stimulus for the whole length of the test did not differ significantly from chance level ($t_{79} = 0.081$; $p = 0.936$).

Finally, as regards the latency to approach one stimulus for the first time during the test, no significant effect of the first stimulus approached was observed ($t_{78} = -0.557$; $p = 0.579$). This meant that chicks were not significantly quicker when approaching the top-heavy or the bottom-heavy stimulus.

Overall, results of the present experiment did not reveal any significant effect (i.e. no index of a preference for one of the two stimuli employed emerged in the present experiment).

At a further level of analysis, we also compared preferences expressed by chicks tested in the present experiment with preferences expressed by chicks tested in Experiment 1[48]. Please note that in Experiment 1 chicks were tested with stimuli identical to those of Experiment 6 in the overall configuration, but presenting the normal direction of contrast polarity expected for a face stimulus (i.e. darker inner features on a lighter face background). This comparison resulted significant as regards both dependent variables that had revealed a significant preference for the face-like stimulus in Experiment 1.

In fact, the number of chicks that approached the face-like configuration when leaving the centre of the apparatus for the first time during the test was significantly different in Experiment 1 with respect to Experiment 6 ($\chi^2_1 = 0.050$; $p = 0.823$), see Graph 8.

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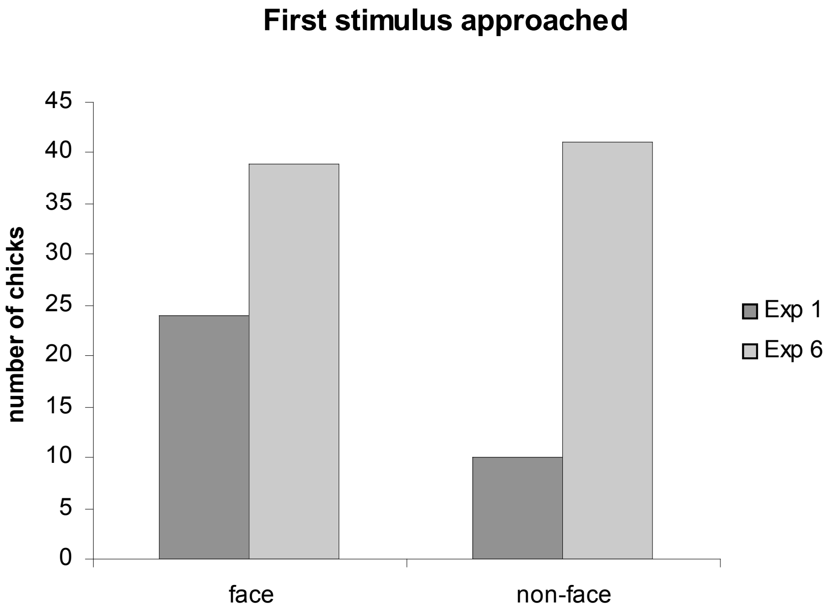
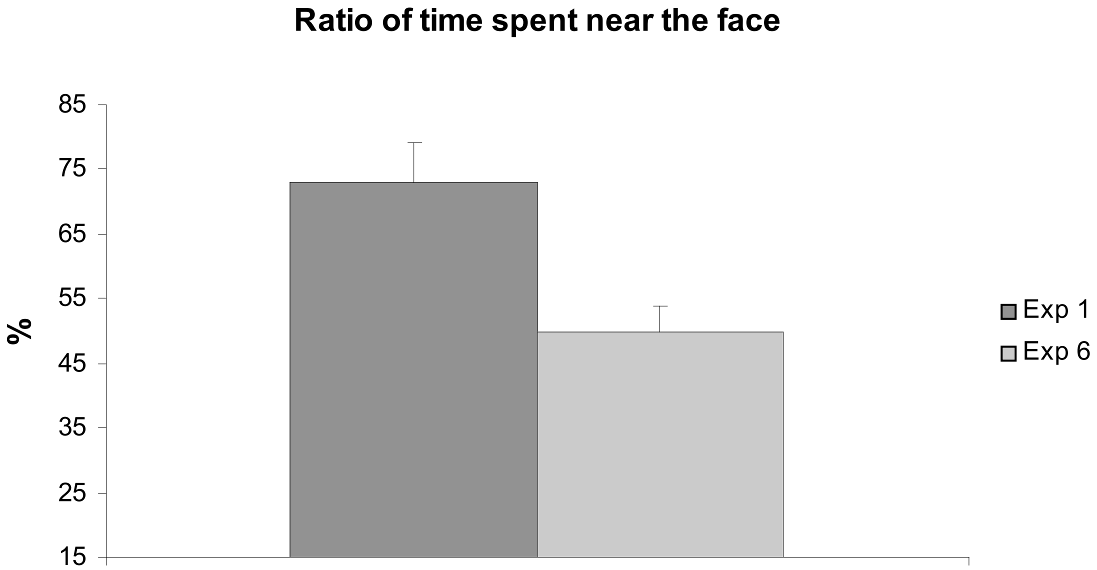
[48] Only the sub-sample of imprinted chicks were used for this analysis.



Graph 8
Number of chicks approaching the face-like (left hand side) versus the non-face-like configuration (right hand side) as first stimulus during the test in Experiment 1 (darker columns) and in Experiment 6 (lighter columns).

Moreover, also as regards the proportion of time spent near the face-like stimulus for the whole length of the test, a significant difference was observed between chicks tested in Experiment 1 and 6 ($t_{112}$ = 2. 812; p = 0.006). See Graph 9.



Graph 9

Mean proportion of time spent near the face-like stimulus in Experiment 1 (darker columns) and in Experiment 6 (lighter column). Group means with SEM are shown.

## Discussion

Results obtained in Experiment 6 demonstrated that the reversal of contrast polarity is effective in abolishing chicks' preference for schematic face-like stimuli, in line with what had been demonstrated in newborn babies (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). In fact, stimuli used in Experiment 6 differed from stimuli used in Experiment 1 only in the direction of contrast polarity (in Experiment 1 the inner features of stimuli were darker than the background, whereas in Experiment 6 the background was darker than the inner features), while all the other features of the test stimuli remained unchanged. This simple modification made the preference for the face-like stimulus (that was evident in Experiment 1) disappear in Experiment 6.

First of all, this result is relevant because it strengthens the existing parallelisms between face-preferences observed in newborn babies and domestic chicks visually naïve with regard to faces (see also Experiment 5). The extent of these parallelisms will be discussed in detail in the "Conclusions" paragraph.

As regards the results obtained in the present experiment, the more likely interpretation seems that proposed by Farroni, Johnson, Menon, Zulia, Faraguna and Csibra (2005) for the effect of contrast polarity reversal in newborn babies. In line with the domain-specific view of newborns' face preferences, Farroni and her colleagues suggest that newborns prefer to look at objects that present the light-shadow pattern (i.e. the pattern of lighter and darker areas) of a face as it appears in a natural environment under natural (top-lit) illumination. The eyes and the mouth are recessed on a face, and thus they appear to be darker than other parts of the face. As a consequence, face-like patterns where the elements within the face are lighter than the background do not elicit face preferences.

We believe that this explanation may apply also to domestic chicks, because this species has shown inborn predispositions to approach objects that are likely to represent a conspecific or another animate creature (see Experiments 1-5 and see also Johnson and Horn, 1985; Vallortigara, Marconato and Regolin, 2005; Vallortigara and Regolin, 2006). Moreover, as already illustrated in Figure 7, the face of a hen or of a chick presents, similarly to the face of a human being, three darker areas (the two eyes and the bill, or the shadow under the bill) on a lighter background. Thus, it is ecologically plausible that chicks' hypothetic face-detection device should be sensitive to the inversion of contrast polarity, similarly to what theorized for newborn babies.

The extent of the analogy between chicks' and human babies' responses to negative images of faces will be investigated in the following experiments.

## Experiment 7

The aim of the present experiment was to try to extend the similarities between human babies' and domestic chicks' responses to negative images of faces (see Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005; and see also Experiment 6).

One very interesting result reported by Farroni and her colleagues concerns the effect of the introduction of a black pupil-like dot within the lighter inner features of the schematic face-like negative stimuli. This simple manipulation restored the original preference for the face-like stimulus in newborn babies. This result has been interpreted by the authors as due to the fact that "…*the function of newborns' orientation bias is to establish eye contact, and human eyes are identified as dark spots within lighter areas (Kobayashi and Kohshima, 1997)…*" thus "… *placing dark 'irises' within the white squares in the negative polarity images should bring the preference … back*" (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005).

Moreover, also the results recently obtained by Gliad, Meng and Sinha (2009) point toward an interesting explanation of this phenomenon observed in newborns. These authors demonstrated that, in human adults, face recognition is mainly influenced by ordinal relationships between luminance levels of areas surrounding the eyes. It has to be noticed that, by adding the pupil-like dot within the stimuli inner features, Farroni and her colleagues also restored the correct ordinal relationships between luminance of the inner face features and luminance of the background, even though only at the local level. In fact, thanks to the addition of the pupil-like dot, the face-like stimulus presented again a triangular configuration of dark elements (the black dots) on a lighter background (in this case the lighter background was constituted by the three white squares that represent the inner features of the stimuli).

The aim of Experiment 7 was to investigate whether it was possible to observe this same effect, obtained in newborn babies by Farroni and her colleagues, also in domestic chicks.

### *Subjects*

Subjects were 67 (34 male and 33 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

Test stimuli employed for Experiment 7 were identical to those used in Experiment 6, except that stimuli used in Experiment 7 presented a darker blob within the lighter face inner features (a square of 0.3 x 0.3 cm). See Figure 35.

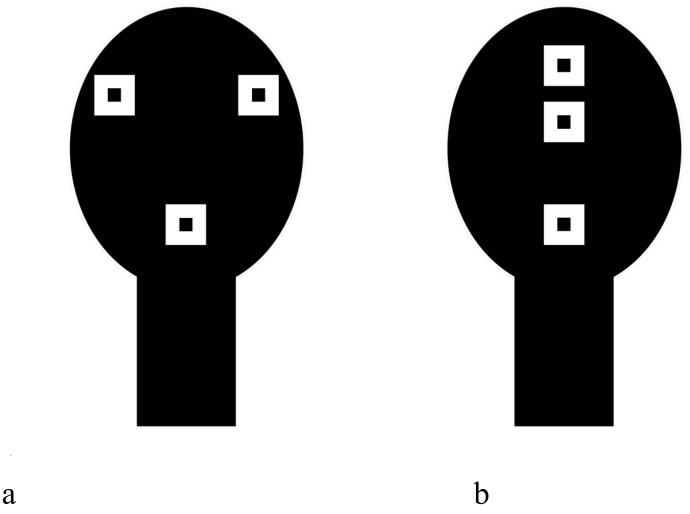


Figure 35

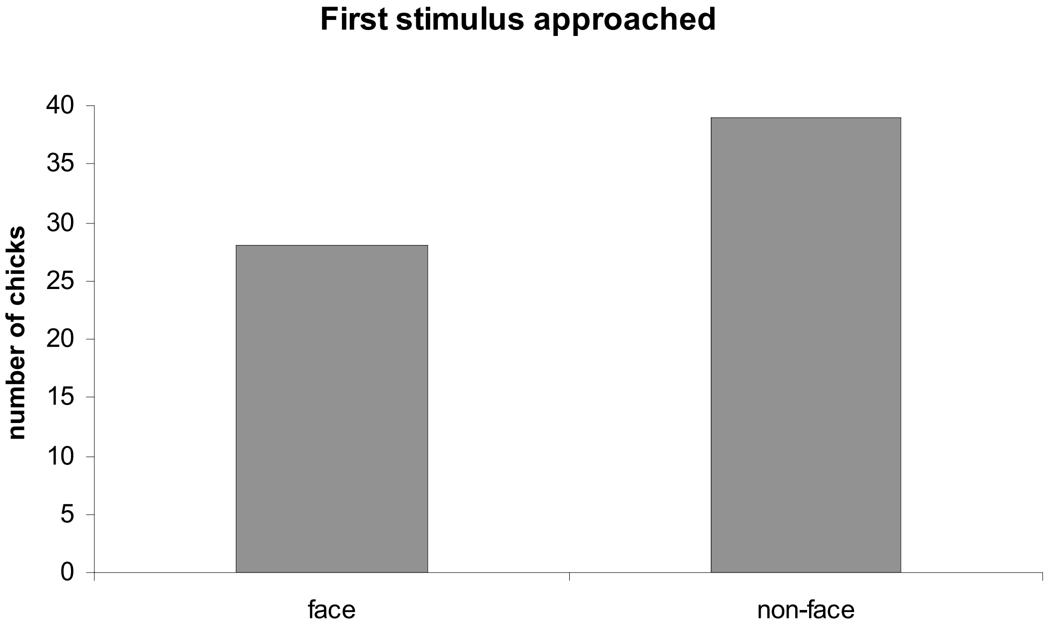
Representation of the stimuli used in Experiment 7. Stimulus a) was obtained from the face-like stimulus used in Experiment 6, whereas stimulus b) was obtained from the non-face-like stimulus of Experiment 6. The only difference with respect to the stimuli used in Experiment 6 is the presence of a darker blob, added within each of the lighter inner features of the stimuli.

Such blob was added within face features in order to correspond to the pupil-like dot employed in the stimuli successfully employed by Farroni, Johnson, Menon, Zulia, Faraguna and Csibra (2005) to restore the preference for the face-like stimulus in configurations having a negative contrast polarity. As already mentioned above with regard to the stimuli employed by Farroni and her colleagues, this manipulation also has the effect of restoring the correct ordinal relationships between luminance of the inner face features and luminance of the background, at least at the local level. In stimuli used for Experiment 7, in fact, the darker blobs created a triangular configuration of darker areas on the lighter backgrounds of the inner features.

Thus, our hypothesis was that, due to the presence of the darker blob within the inner face features, chicks' preference for the face-like stimulus should re-emerge in the present experiment. In fact, this outcome seemed likely in consideration of both the results previously obtained in newborns by Farroni and her collaborators (2005), and in consideration of the hypothesis proposed by Gliad, Meng and Sinha (2009) as regards the central role, for face perception, of ordinal relationships between luminance levels of areas surrounding the eyes.

### *Results*

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the face-like first was not significantly different from the number of chicks that approached the non-face-like configuration first ($\chi^2_1 = 1.806$; $p = 0.179$; 28 chicks approached the face, 39 the non-face), though there was a trend towards a preference for the non-face-like stimulus. See Graph 10.

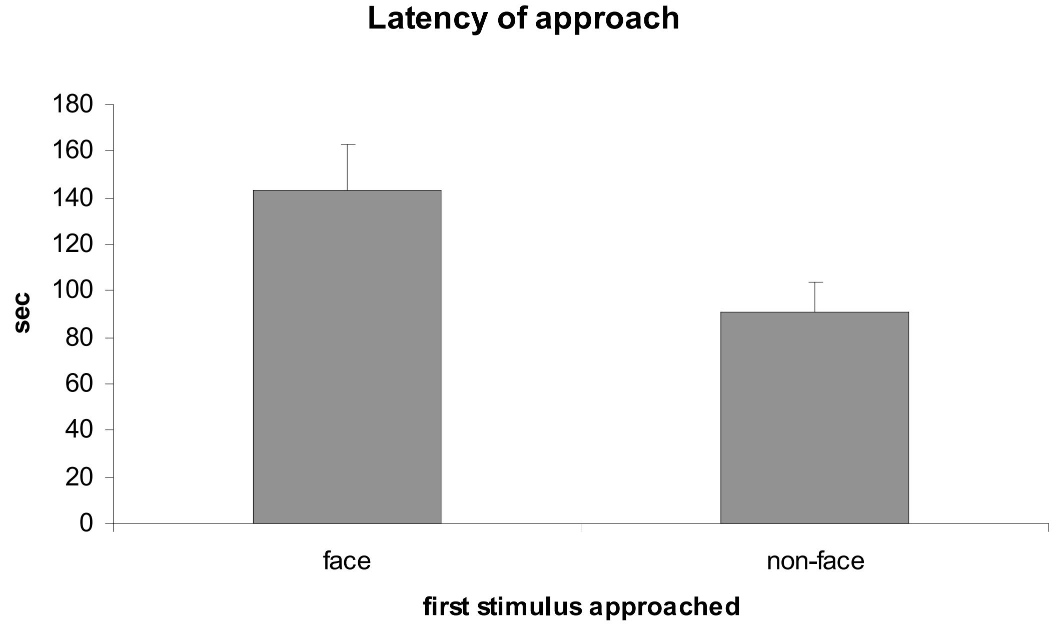


Graph 10

Number of chicks approaching the face-like (left hand side) versus the non-face-like configuration (right hand side) as first stimulus during the test in Experiment 7.

Moreover, the proportion of time spent near the face-like stimulus for the whole length of the test did not differ significantly from chance level ($t_{66} = -0.129$; $p = 0.898$).

However, as regards the latency to approach one stimulus when leaving the centre of the apparatus for the first time during the test, a significant effect of the first stimulus approached emerged. In fact, chicks approaching the face-like stimulus were significantly slower than chicks approaching the non-face-like stimulus first ($t_{65} = 2.154$; $p = 0.035$). See Graph 11.



Graph 11

Mean latency of first approach in Experiment 7, for chicks approaching the face-like stimulus (left hand side column) and for chicks approaching the non-face-like one (right hand side column). Group means (in seconds) with SEM are shown.

### *Discussion*

Results obtained in Experiment 7 are not of immediate interpretation. If on the one hand the stimuli employed in this experiment were somewhat effective in eliciting a preference for one of the two stimuli (in contrast to what observed in Experiment 6), on the other hand the preference observed was in the opposite direction with respect to our prediction. In fact, our chicks showed a preference for the non-face-like stimulus, being quicker in approaching this stimulus. This effect may seem quite puzzling. We believe that an interpretation is nevertheless possible for the results that we obtained, based also on the fact that the preference demonstrated by our chicks was evident for the dependent variable latency to approach, that is a measure often associated with fear responses induced by the presence of predator-like stimuli. Moreover, in the literature it is known that domestic chicks are spontaneously frightened by the presence of stimuli that resemble one pair of eyes (e.g. Gagliardi, Gallup and Boren, 1976; Gallup, Nash, Donegan and McClure, 1971; Gallup, Nash and Ellison, 1971; Scaife, 1976). This kind of response possibly evolved as part of an anti-predatory mechanism, apt to detect stimuli that may reveal the presence of a predator attentive to the chick, in order to induce freezing defensive responses. Such anti-predatory fear responses induced by eye-like objects are present also in young chicks that are visually naïve with respect to this kind of stimuli (Rosa Salva, Regolin and Vallortigara, 2007). It is important to note that some visual features of stimuli can determine whether they will be perceived as eye-like objects, and thus whether they will elicit a fear response in chicks. For example, the presence of a darker pupil contrasting with a lighter iris is a crucial element for eye-like stimuli to be effective in eliciting the fear response in chicks (Gallup, Nash and Ellison, 1971). An interesting study by Jones (1980) demonstrated that some features of two-dimensional eye-shapes are crucial in order to elicit avoidance in 1-week old chicks. In particular, factors such as horizontal orientation (presence of two eyes aligned on the same horizontal line instead of aligned on a vertical line), pairedness of the eyes (presence of 2 eyes instead of 3 eyes or 1 eye) and presence of both iris and pupil, were crucial in order to observe a fear response in chicks.

We thus reasoned that the face like-stimulus employed in Experiment 7 might have elicited an anti-predatory fear response in the chicks that we tested, due to the fact that its two upper features resembled a pair of predatory eyes. In fact, conspicuous eyes are a distinctive trait of many potential predators. In many predator species, the dark spot created by the iris-pupil against the white sclera creates a distinctive luminance pattern characterised by a concentric organization of the two areas having different luminance. In such predator species the inner area has usually a lower luminance (i.e. is darker) than the outer area (see Figure 5). Thus, by adding the dark pupil-like blob within the lighter inner features of our stimuli, we gave to the inner features the appearance of the eyes of a potential predator. However, only in the face-like stimulus such eye-like features were presented as horizontally oriented (Jones, 1980). Thus, the effect we observed could have been due to a fear response elicited in chicks by the pair of “predatory eyes” that the face-like stimulus presented. This hypothesis was further tested in Experiments 8-11.

## Experiment 8

In Experiment 7 we obtained evidence of a preference for the non-face-like stimulus. We hypothesised that this result could be due to an anti-predatory fear reaction induced by the face-like stimulus, due to the fact that its two upper features resembled a pair of predator's eyes (see above, Discussion of Experiment 7).

In the present experiment we decided to test this hypothesis, by using a pair of stimuli that should be more effective in eliciting a fear response in chicks. In fact, Gagliardi, Gallup and Boren (1976) found evidence that one specific value of the pupil-to-eye ratio (11/20) is the most effective in inducing fear reactions to eye-like shapes in chickens. We thus decided to use a pair of stimuli that presented the appropriate pupil-to-eye ratio, in order to verify whether with this pair of stimuli we could observe a more pronounced avoidance response for the face-like stimulus.

### *Subjects*

Subjects were 37 (18 male and 19 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

Test stimuli employed for Experiment 8 were identical to these used in Experiment 7, except that in Experiment 8 the pupil-like blob within the lighter face inner features was larger than in Experiment 7 (0.5 x 0.5 cm).

In this way we modified the pupil-to-eye ratio (i.e. the ratio between the dimension of the darker pupil-like blob and that of the lighter face inner features) in order to obtain a ratio of approximately 11/20. This ratio has in fact been proved to be the most effective in eliciting a fear reaction to eye-like-shapes in domestic chicks (Gagliardi, Gallup and Boren, 1976). In Experiment 7 the ratio was instead of about 6.6/20.

See Figure 36.

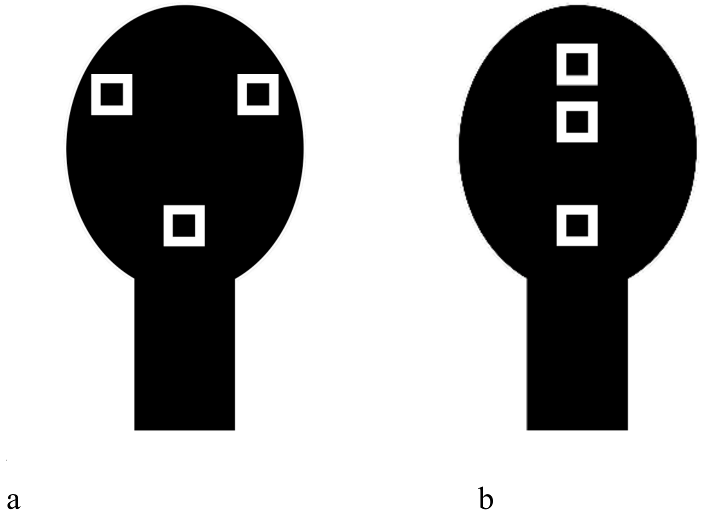
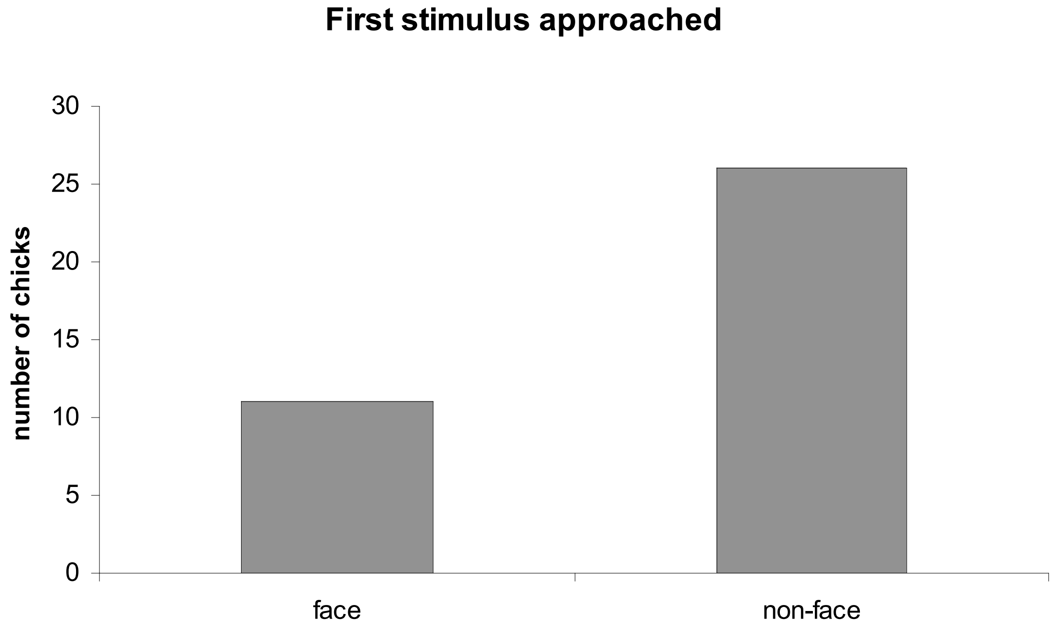


Figure 36
Representation of the stimuli used in Experiment 8. Stimulus a) was obtained from the face-like stimulus used in Experiment 7, whereas stimulus b) was obtained from the non-face-like stimulus of Experiment 7. The only difference with respect to the stimuli used in Experiment 7 is the dimension of the pupil-like blob, which has been increased in with respect to the same feature stimuli used in the previous experiment.

Our hypothesis was that using this pair of stimuli, which is potentially more fear inducing than those used in Experiment 7 due to the presence of the appropriate pupil-to-iris ratio, we should confirm and extend the effect of avoidance of the face-like stimulus observed in the previous experiment.

### *Results*

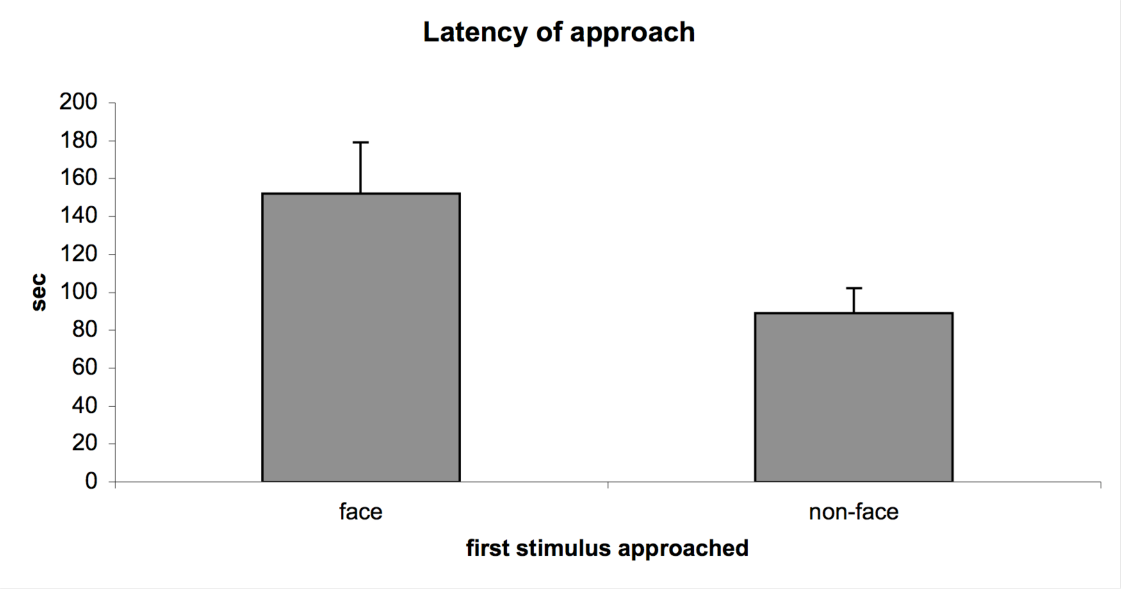
As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the non-face-like configuration as the first stimulus was significantly higher than the number of chicks that approached the face-like configuration ($\chi^2_1 = 6.081$; $p = 0.014$; 11 chicks approached the face-like stimulus and 26 the non-face-like stimulus). See Graph 12.



Graph 12

Number of chicks approaching the face-like stimulus (left hand side) versus the non-face-like stimulus (right hand side) as first stimulus during the test in Experiment 8.

However, the ratio of time spent near the face-like configuration was not significantly different than what expected by chance level ($t_{36} = 0.385$; $p = 0.703$). Nevertheless, as regards the latency to approach one stimulus when leaving the centre of the apparatus for the first time during the test, a significant effect of the first stimulus approached emerged. In fact, chicks approaching the non-face-like stimulus were significantly quicker than chicks approaching the face-like stimulus first ($t_{35} = 2.266$; $p = 0.030$). See Graph 13.



Graph 13

Mean latency of first approach in Experiment 8, for chicks approaching the face-like stimulus (left hand side column) and for chicks approaching the non-face-like one (right hand side column). Group means (in seconds) with SEM are shown.

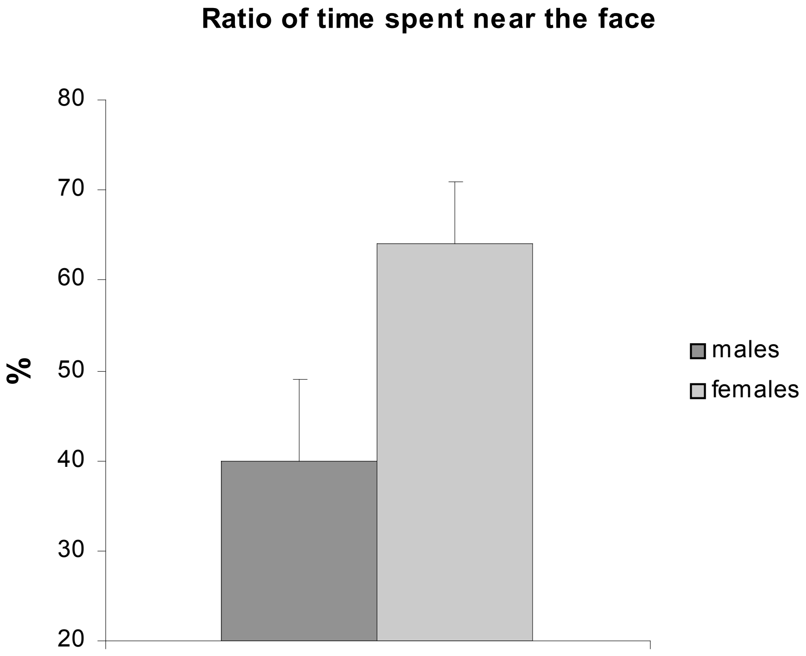
Thus, the results observed up to the present moment led us to confirm the post-hoc hypothesis that the effects we observed (i.e. a preference for the non-face-like stimulus) were due to a fear reaction elicited by the resemblance of the two upper features of the face-like stimulus with the appearance of a pair of predator's eyes.

On the basis of such a post-hoc hypothesis we decided to investigate also the effect of sex on chicks' preferences, limitedly to the present experiment. In fact, gender differences are often present in fear responses (usually fear responses result more pronounced in males) (Jones, 1977).

As regards the first stimulus approached, we did not observe any significant difference in the number of male and female chicks that approached the face-like or the non-face-like stimulus, when leaving the centre of the apparatus for the first time during the test ($\chi^2_1 = 0.946$, $p = 0.331$; 4 males approached the face-like stimulus and 14 the non-face-like one; 7 females approached the face-like stimulus and 12 the non-face-like one). Similarly, also as regards the latency to approach one stimulus when leaving the centre of the apparatus for the first time during the test, no significant effect of sex or interaction with the first stimulus approached was observed (*first stimulus approached* $F_{(1,33)}$ =

6.649, p = 0.015; *sex* $F_{(1,33)}$ = 2.751, p = 0.107; *first stimulus approached * sex* $F_{(1,33)}$ = 0.405, p = 0.529).

However, as regards the ratio of time spent near the face-like stimulus for the whole length of the test, a marginally non-significant effect of sex was observed in the direction that we hypothesised ($t_{35}$ = -1,920; p = 0.063). In fact, males tended to spend more time near the non-face-like stimulus, whereas females tended to spend more time near the face-like one. See Graph 14.



Graph 14

Mean proportion of time spent near the face-like stimulus in Experiment 8, for male (darker column) and female (lighter column) chicks. Group means with SEM are shown.

## *Discussion*

Results obtained in Experiment 8 confirmed and extended those of Experiment 7. Chicks tested with the new pair of stimuli employed in Experiment 8, which were designed in order to be more effective in eliciting a fear reaction with respect to stimuli used in Experiment 7 (Gagliardi, Gallup and Boren, 1976), showed a more clear preference for the non-face-like stimulus. In fact, chicks were quicker when approaching the non-face-like stimulus with respect to when approaching the face-like one, confirming the main finding of Experiment 7. Moreover, the preference for the non-face-like stimulus was evident also as regards a second dependent variable, namely the first stimulus approached by chicks, extending the results obtained in Experiment 7. This may indicate that the fear reaction observed in Experiment 8 was more intense than that observed in Experiment 7, in line with what predicted by the literature on the fear reactions to eye-like shapes in chickens. In fact, stimuli used in Experiment 8 were designed in order to better approximate the pupil-to-iris ratio that has been proved to be the most effective in eliciting a fear reaction in domestic chickens (Gagliardi, Gallup and Boren, 1976).

Finally, on the basis of the post-hoc hypothesis that the effects observed in Experiment 7 and 8 were actually due to fear reactions induced by the face-like stimulus, due to its upper inner features' resemblance with a pair of predatory eyes, we decided to check for the presence of gender differences in chicks' reactions to the two stimuli. In fact, fear reactions in this species are often more pronounced in males (Jones, 1977). A marginally not significant trend was observed, as regards the ratio of time spent near the two stimuli, in the direction of a more pronounced avoidance of the face-like stimulus in males, in line with our speculation. On the ground that marginally non-significant results should be interpreted with caution, we believe that this could provide a further element in favour of our hypothesis that the effects observed are actually due to fear reactions. It should also be noticed that the present experiment had not been designed in order to conduct gender comparisons, which emerged only as a consequence of a post-hoc hypothesis, and thus the sample size could not be optimal for revealing such liable gender differences.

## Experiment 9

In Experiments 7 and 8 we have obtained evidence in favour of the hypothesis that chicks perceived eyes as frightening and in particular that adding a dark pupil-like blob within the inner features of negative schematic faces caused a fear reaction in chicks (see above).

The aim of the present experiment is to further investigate this finding, by checking whether any lateralization effect can be observed in the avoidance of the face-like stimulus showed by domestic chicks. In fact, evidence is there in the literature showing that in domestic chickens, as well as in other species, fear reactions and anti-predatory responses are lateralized in favour of a control by the right hemisphere (Andrew, 1991; Andrew, Mench and Rainey, 1982; Phillips and Youngren, 1986; Rogers, 1997; Rogers, 2000; Rogers, Zucca and Vallortigara, 2004). Moreover, in a previous study we obtained evidence that, in particular, fear reactions induced by the eye gaze of a potential predator would be lateralized in favour of the right hemisphere, in domestic chicks (Rosa Salva, Regolin and Vallortigara, 2007).

In the present experiment we thus decided to test chicks using the same stimuli employed in Experiment 8, but limiting chicks' vision at test to one eye. Testing chicks under such monocular vision condition is a standard technique employed to investigate brain lateralization in this species. In fact, monocular eye-patching allows the effective limitation of chicks' visual processing to the hemisphere contralateral to the eye in use (see below).

### ***Subjects***

Subjects were 46 (23 male and 23 female) domestic chicks (*Gallus gallus domesticus*).

### ***Test stimuli***

Test stimuli employed in Experiment 9 were identical to those used in Experiment 8, as these were the most effective in eliciting a fear reaction toward the face-like stimulus, see above.

### ***Experimental procedures used to test brain lateralization***

The development and behavioural effects of brain lateralization have been extensively studied in domestic chicks (see Rogers, 1995; Vallortigara, 1994). Lateralization of the chick's brain is triggered by exposure of the embryo within the egg to the environmental light (Rogers and Sink, 1988). During development, the embryo turns so that the right eye faces outward, toward the translucent egg shell and to any available light. At the same time the left eye is turned toward the body mass and receives little or no light. Whilst still in the egg, a visual pathway in the chick, known as the thalamofugal pathway, undergoes differentiation. During a critical period (from embryonic day 17 to 21; see Rogers, 2008) exposure to light produces an asymmetrical stimulation of the two eyes such that there is an increase in forebrain projections from the left side of the thalamus (fed by the light stimulated right eye) compared with the right side (Rogers and Deng, 1999; Koshiba, Nakamura, Deng and Rogers, 2003). It is thought that as little as 2 hours exposure to light prior to hatching is sufficient to induce these brain asymmetries (Rogers, 1997). However, if the chick does not receive light during incubation, this lateralization is largely prevented[49] (see Rogers and Bolden, 1991).

Moreover, in domestic chickens anatomical lateralization and its behavioural correlates remain largely confined to each hemisphere, since the avian brain does not have a corpus callosum and displays a virtually complete decussation of optic fibres at the optic chiasm (Csillag and Montagnese, 2005). Methodologically speaking, this means that visual input to the chick's brain can be restricted to one hemisphere without the need for invasive surgical procedures. Specifically, a simple patch over one eye can be used to discern hemisphere specializations (Rogers, 1997; Gülbetekin, Güntürkün, Dural and Cetinkaya, 2007). This non-invasive procedure, called monocular occlusion procedure, is employed in Experiment 9 in order to investigate functional lateralization in chicks' responses test stimuli.

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[49] Nevertheless, there are some forms of lateralization in chicks that do not depend on light exposure of the embryo, including social recognition (Deng and Rogers, 2002), response to olfactory versus visual cues (Rogers, Andrew and Burne, 1998) and components of object or spatial-specific cues (Chiandetti, Regolin, Rogers and Vallortigara, 2005; see also Vallortigara and Rogers, 2005).

Thus, in Experiment 9, the standard procedures described in the “General materials and methods” paragraph were altered in order to investigate lateralization in chicks’ responses. These alterations to the general procedure will be described in the following paragraphs.

In the present experiment we tested chicks hatched from eggs that had been exposed to light from the 17th to the 19th day of incubation, in order to lateralize chicks’ visual pathways. The incubator light was always turned off before the chicks started to hatch, and thus hatching took place in complete darkness.

Moreover, approximately 30 minutes before the test, chicks were temporarily eye patched (by using a removable, sticky tape), in order to obtain two groups of chicks in monocular vision conditions. The eye patching was in fact performed on one eye only, leaving the other eye free and perfectly able to see. The eye-patching procedure is a relatively minor procedure for the animals, requiring handling for only a few seconds: it consists of gently placing the removable tape over one eye (the tape is cup-shaped and does not prevent the normal movements of the chicks’ eyelid). Nevertheless, the eye-patching procedure was performed only after placing each chick in a “one-way screen box”, in order to prevent chicks any visual experience of the experimenters’ face during the eye-patching. The upper side of this box was a one-way screen that allowed the experimenter to see the chick within the box, whereas the chick could not see the experimenter standing near to the box. The inside of the box was illuminated by two 15 W-240 V lamps placed within the box, whereas the rest of the room where the box was located was in complete darkness. On one of the lateral sides of the box a hole was present, in order to allow the experimenter to insert his/her hands within the box, to eye-patch the chick.

As mentioned above, following the eye-patching procedure, all chicks were allowed approximately 30 min in order to become accustomed to the new monocular condition, before the test took place. Chicks were then tested under monocular vision condition, and the eye-patching was removed only at the end of the test.

Each chick was tested only once, as for all prior experiments. Thus, each chick participated only to one monocular vision condition. In particular, 23 chicks (11 males and 12 females) had their right eye patched, and thus their left eye in use, whereas other 23 chicks (12 males and 11 females) had their left eye patched, and thus their right eye in use. Chicks using their right eye will be referred to as RE chicks, and are assumed to process visual stimuli mainly with their left hemisphere. On the contrary, chicks using their left eye will be referred to as LE chicks, and are assumed to process visual stimuli mainly with their right hemisphere.

All other aspects of the experimental procedure were exactly as described in the “General materials and methods”.

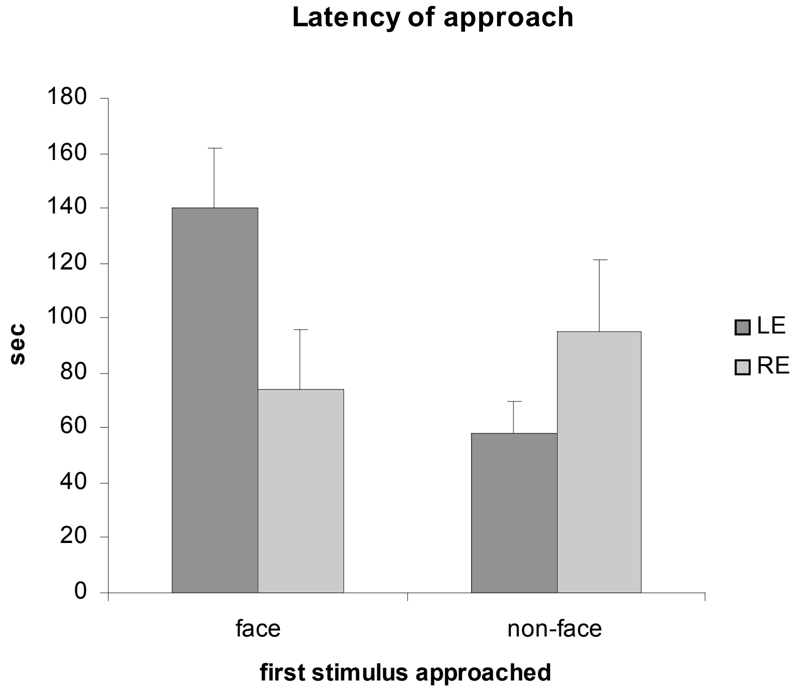
### *Results*

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the face-like configuration or the non-face-like configuration was not significantly different for LE and RE chicks ($\chi^2_1$ = 0.783; p = 0.376). Overall, the number of chicks that approached the non-face-like configuration was the same as the number of chicks that approached the face-like configuration ($\chi^2_1$ = 0.000; p = 1.000; 23 chicks approached the non-face-like configuration and 23 the face-like-one).

In line with this evidence the ratio of time spent near the face-like stimulus for the whole length of the test was not significantly different between LE and RE chicks ($t_{44}$ = 1.494; p = 0.142). Thus the ratio of time spent near the face-like stimulus was compared with chance level for the overall sample, and the comparison resulted not significant ($t_{45}$ = -0.054; p = 0.957).

However, as regards the latency to approach one stimulus when leaving the centre of the apparatus for the first time during the test, a significant interaction between the factors *first stimulus approached* and *eye in use* was observed ($F_{(1,42)}$ = 5.127; p = 0.029). From this interaction it was evident that LE chicks were significantly slower when approaching the face-like stimulus (thus confirming the result obtained in Experiments 7 and 8), whereas in RE chicks this trend was absent. See Graph 15.

All main effects were non significant (*first stimulus approached* $F_{(1,42)}$ = 1.821; p = 0.184), (*eye in use* $F_{(1,42)}$ = 0.402; p = 0.503).



Graph 15

Mean latency of first approach in Experiment 9, for chicks approaching the face-like stimulus (left hand side) and for chicks approaching the non-face-like one (right hand side). Latencies are presented separately for LE (darker columns) and RE (lighter columns) chicks. Group means (in seconds) with SEM are shown.

### *Discussion*

Results obtained in Experiment 9 confirmed and extended those of Experiments 7 and 8. In fact, also in Experiment 9 a significant avoidance of the face-like stimulus was observed for the dependent variable latency of approach (a dependent variable often associated with fear responses, see e.g. Rosa Salva, Regolin and Vallortigara, 2007).

Even more relevantly, however, this effect was actually limited to chicks having their left-eye in use (LE chicks), and thus elaborating visual information mainly with the right hemisphere. This result confirmed our initial hypothesis that the preference for the non-face-like stimulus observed in Experiments 7-8, would be actually caused by an avoidance of the face-like stimulus, due to a fear reaction to the eye-like appearance of its two upper features. In fact, anti-predatory responses and fear reactions in general are lateralized in favour of the right hemisphere, in chicks and other species. Indeed, Phillips and

Youngren (1986) demonstrated, using biochemical interventions, that the right hemisphere is involved in the control of avian fear behaviour. In line with this evidence, it has been shown that fear responses to predators are much quicker or more pronounced when the predator is detected by the left eye than by the right eye of domestic chicks (Andrew, Mench and Rainey, 1982; Rogers, 1997 for a review; Rogers, 2000; Rogers, Zucca and Vallortigara, 2004). In fact, the left eye is preferentially used to scan for a predator after detection of its presence (Evans, Evans and Marler, 1993) and, using the left eye system, chicks are quicker to detect the predator when engaged in a dual task paradigm (selective feeding together with predator detection; Rogers, Zucca and Vallortigara, 2004). Even more relevant for the results of the present experiment is the evidence, previously obtained in our laboratory, that the right hemisphere of domestic chicks is dominant for fear responses to the direct gaze of a potential predator (a human-like dummy face) (Rosa Salva, Regolin and Vallortigara, 2007). It should be noticed that the chicks tested by Rosa Salva, Regolin and Vallortigara, 2007 were visually naïve with respect to eye-gaze (exactly as those used in the present experiment).

Thus, results obtained in the present experiment, together with those of Experiments 7-8, indicate that, in domestic chicks, an avoidance reaction (mainly evident in the latency to approach stimuli) can be induced by adding a dark pupil-like blob within the inner features of a negative schematic face. Moreover, in line with previous evidence available in the literature (see above), the right hemisphere seems to be dominant for such a fear reaction.

However, it remains to be investigated whether such a fear reaction is evident only when stimuli are negative versions of schematic faces (i.e. only if stimuli present reversed contrast polarity with respect to normal faces). This issue will be investigated in Experiments 10-11.

## Experiment 10

The aim of the present experiment was to investigate whether chicks' avoidance reactions to the face-like stimuli employed in Experiments 7-9 could be elicited also by similar stimuli that differ from those of Experiments 7-9 only in that they present the normal direction of contrast polarity for a face. For this reason, in Experiment 10 we employed stimuli that presented both predator-eye-like inner features identical to those of stimuli used in Experiments 8-9, and the normal direction of contrast polarity expected for a face.

Our hypothesis was that, in this circumstance, an avoidance of the face-like stimulus should be observed, in line with the results obtained in Experiments 7-9. This prediction was based on the fact that the stimulus used in Experiment 10 presented identical inner features with respect to stimuli used in Experiments 8-9 (data of previous experiments, in fact, seemed to indicate that stimuli inner features were the crucial factor in order to elicit an avoidance of the face-like stimulus in chicks).

The present experiment was devised in order to test this hypothesis. In Experiment 10, unlike in Experiment 9, we did not aim to investigate brain lateralization, thus chicks were normally tested with both eyes in use and according to the standard procedures described in the "General materials and methods".

### *Subjects*

Subjects were 52 (24 male and 28 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

Test stimuli used in Experiment 10 were obtained from those of Experiments 8-9. In particular, stimuli used in Experiment 10 presented identical predator-eye-like inner features with respect to those used in Experiments 8-9. This was done in order to obtain a pair of stimuli whose inner features would be the most effective in eliciting an anti-predatory fear reaction in chicks (see Experiments 7 and 8). However, stimuli used in the present experiment differed from those of Experiments 7 and 8, because they were modified in order to restore the normal direction of contrast polarity expected for a face. See Figure 37.

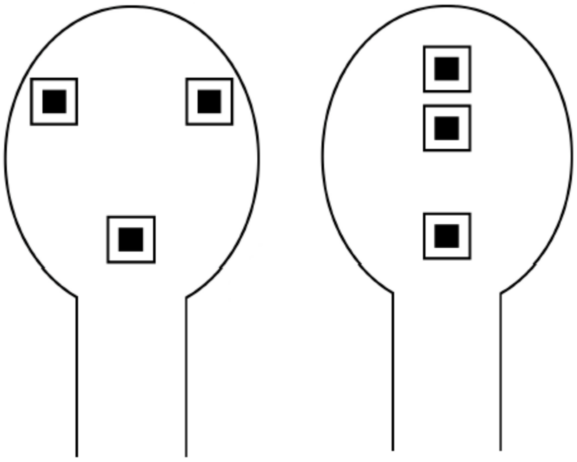

a b

Figure 37
Representation of the stimuli used in Experiment 10. Stimulus a) is a face-like configuration modified from that used in Experiments 8-9, whereas stimulus b) is a non-face-like configuration modified from that used in Experiments 8-9. However, unlike stimuli used in Experiments 8-9, both stimulus a) and b) present the normal direction of contrast polarity expected for a face, i.e. darker inner face features on a lighter face back-ground.

Using this new pair of stimuli we were therefore able to investigate how chicks could react to the presence of predator-eye-like inner features, when such features are embedded within a face-like configuration having the normal direction of contrast polarity expected for a face (see above).

***Results***

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the non-face-stimulus was not significantly different from the number of chicks that approached the face-like one ($\chi^2_1 = 0.308$; $p = 0.788$; 24 chicks approached the face and 28 the non-face).

Moreover, in line with the above mentioned result, the proportion of time spent near the face-like stimulus for the whole length of the test did not differ significantly from what expected by chance ($t_{51} = -0.270$; $p = 0.788$).

Finally, as regards the latency to approach one stimulus for the first time during the test, no significant effect of the first stimulus approached was observed ($t_{50} = -1.273$; $p = 0.209$). This meant that chicks were not significantly quicker when approaching the non-face-like or the face-like stimulus.

Overall, results of the present experiment did not reveal any significant effect (i.e. no index of a preference for one of the two stimuli employed emerged), in contrast to what observed in Experiment 8.

### *Discussion*

The aim of the present experiment was to investigate how chicks would react to the presence of predator-eye-like inner features, when such features are part of a face-like configuration having the normal contrast polarity of a face (see Figure 37). Results obtained are in contrast to what observed both in Experiment 8 and in Experiment 1. In fact, no significant preference for one of the two stimuli was evident in chicks tested in Experiment 10.

Before running the present experiment we predicted that chicks would show an avoidance of the face-like stimulus. This prediction was mainly based on the results obtained in Experiments 7-9, indicating that stimuli inner features were the crucial factor in chicks' avoidance of the face-like stimulus. Our original hypothesis was, in fact, that the mere presence of two inner features resembling the eyes of a predator could be enough to elicit an avoidance reaction in chicks.

This prediction was, however, founded on the assumption that chicks would simply react to the presence of predator-eye-like inner features in the face-like stimulus, and avoid such stimulus, regardless of its overall contrast polarity. Results obtained in the present experiment did not confirm our initial hypothesis.

On the grounds that non-significant results should be interpreted with caution, we believe that it is all the same possible to propose an interesting explanation for the evidence obtained in Experiment 10.

Contrary to the underlying assumption of our original hypothesis, we believe that results of Experiment 10 show that contrast polarity is a relevant factor in chicks' preferences (in line with data obtained in Experiment 6). In particular we believe that, in the present experiment, by restoring the original contrast polarity of the stimuli, we restored the perception of the face-like stimulus as a face (and thus as an appropriate social stimulus). This in turn could restore the original preference for the face-like stimulus (see Experiment 1). However, no such a preference was evident in Experiment 10. This outcome was probably due to the simultaneous presence, in chicks, of two opposite and conflicting tendencies: a social preference for the face-like stimulus, and an anti-predatory avoidance response elicited by the eye-like appearance of the two upper features of the same stimulus.

A further element of interest in the results of Experiment 10 is, thus, that evidence obtained in the present experiment supports, even though indirectly, the claim that the direction of contrast polarity is a crucial factor in chicks' face preferences. In fact, restoring the normal direction of contrast polarity, as we did in Experiment 10, was enough to abolish the avoidance of the face-like stimulus that was observed in Experiments 7-9 with negative stimuli.

## Experiment 11

Experiment 10 investigated chicks' preferences when tested with a schematic stimulus presenting both a face-like configuration (with normal contrast polarity) and predator-eye-like inner face features. When confronted with this kind of stimulus chicks behaved as if they were simultaneously experiencing two opposite tendencies: a tendency to approach the face-like configuration and an avoidance response elicited by the predator-eye-like appearance of its two upper features, resulting in the absence of any significant preference for one of the two stimuli.

In the present experiment, in line with what done in Experiment 9, we decided to investigate the presence of functional lateralization in chicks' responses to the stimuli used in Experiment 10, by using the monocular occlusion technique described for Experiment 9, limiting chicks' vision at test to one eye (see above).

On the basis of the results obtained in Experiment 9, we hypothesised that LE chicks (having their right hemisphere in use) would show a more pronounced tendency to avoid the face-like stimulus with respect to RE chicks (having their left hemisphere in use). This outcome would be in line not only with evidence obtained in Experiment 9, but also with other evidence available in the literature on the dominant role of the right hemisphere in anti-predatory fear reactions (Andrew, 1991; Andrew, Mench and Rainey, 1982; Phillips and Youngren, 1986; Rogers, 1997; Rogers, 2000; Rogers, Zucca and Vallortigara, 2004; Rosa Salva, Regolin and Vallortigara, 2007). In this case we would expect a significant difference between LE and RE chicks to be evident as regards the dependent variable latency of approach (often sensitive to fear reactions, see also Experiments 7-9).

Experiment 11 was thus devoted to investigate the hypothesis described above.

### *Subjects*

Subjects were 73 (36 male and 37 female) domestic chicks (*Gallus gallus domesticus*).

### *Test stimuli*

Test stimuli employed in Experiment 11 were identical to those used in Experiment 10, in order to be able to investigate lateralization effects associated with this pair of stimuli.

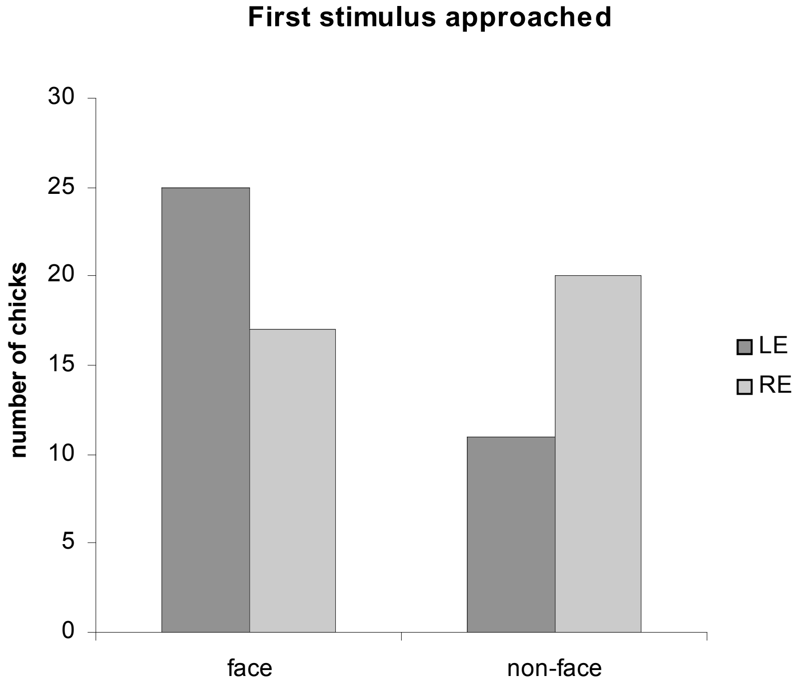
### *Experimental procedures used to test brain lateralization*

In Experiment 11, exactly as in Experiment 9, the standard procedures described in the “General materials and methods” were altered in order to investigate lateralization in chicks’ responses to the stimuli here employed. The alterations to the general procedure introduced to investigate brain lateralization in the present experiment are the same as those described for Experiment 9. All other aspects of the experimental procedure were exactly as described in the “General materials and methods”.

In the present experiment, 36 chicks (18 males and 19 females) had their right eye patched, and thus their left eye in use (LE chicks). Other 37 chicks (18 males and 19 females) had their left eye patched, and thus their right eye in use (RE chicks).

### *Results*

As regards the stimulus approached by chicks when leaving the centre of the apparatus for the first time during the test, the number of chicks that approached the non-face-like configuration or the face-like configuration was significantly different for LE and RE chicks ($\chi^2_1 = 4.124$; $p = 0.042$). See Graph 16. Thus, the number of chicks approaching the face-like and the non-face-like stimulus when leaving the centre of the apparatus for the first time during the test was investigated separately for LE and RE chicks. This comparison resulted significant for LE chicks that preferred to approach the face-like stimulus ($\chi^2_1 = 5.444$; $p = 0.020$; 25 chicks approached the face and 11 chicks approached the non-face-like stimulus). On the contrary, for RE subjects the number of chicks approaching the face-like or the non-face-like stimulus was not significantly different ($\chi^2_1 = 0.243$; $p = 0.622$; 17 chicks approached the face and 20 chicks approached the non-face-like stimulus).



Graph 16

Number of chicks approaching the face-like (left hand side) versus the non-face-like configuration (right hand side) as first stimulus during the test in Experiment 11, separately for LE chicks (darker columns) and RE chicks (lighter columns).

However, the proportion of time spent near the face-like stimulus for the whole length of the test did not differ significantly between LE and RE chicks ($t_{71}$ = 1.247; p = 0.207). Thus, the ratio of time spent near the face-like stimulus was compared to chance level for the overall sample. This comparison resulted non-significant ($t_{72}$ = 0.387; p = 0.700).

Moreover, as regards the latency to approach one stimulus for the first time during the test, no significant effect of the factors *first stimulus approached* or of *eye in use* or any significant interaction was observed (*first stimulus approached* $F_{(1,69)}$ = 0.707; p = 0.403; *eye in use* $F_{(1,69)}$ = 0.740; p = 0.393; *first stimulus approached * eye in use* $F_{(1,69)}$ = 1.093; p = 0.299). This meant that chicks were not significantly quicker when approaching the non-face-like over the face-like stimulus and that no difference was present between LE and RE chicks on this regard.

### ***Discussion***

The results of the present experiment confirmed some of the evidence that was previously obtained in other experiments described in this thesis. In fact, in Experiment 11, as in Experiment 9 a lateralization effect was demonstrated as regards chicks' preferences for schematic face-like stimuli, confirming that the task and stimuli that we employed are appropriate for the investigation of brain lateralization. Moreover, in Experiment 11, as already in Experiment 1, we observed a preference for approaching a face-like stimulus composed of darker inner features on a lighter face background.

A most interesting comparison is that between results obtained in the present experiment in LE and RE chicks and results that were obtained in binocular chicks in Experiment 10. In fact, in Experiment 10, binocular chicks did not display any significant preference for one of the two test stimuli (identical to those of the present experiment). We hypothesised that this could have been due to the fact that chicks simultaneously experienced two opposite tendencies: a tendency to approach the face-like configuration presenting the normal contrast polarity for a face and an avoidance response elicited by the predator-eye-like appearance of its two upper features. Results of the present experiment support at least in part this interpretation, showing that one of these two tendencies (i.e. the predisposition to approach face like-stimuli) emerged in LE chicks.

However, the preference demonstrated by LE chicks was in the opposite direction with respect to our initial prediction. In fact, on the basis of results obtained in Experiment 9 and of other evidence available in the literature on the dominant role of the right hemisphere in anti-predatory fear reactions (see above), we had predicted that LE chicks would show a tendency to avoid the face-like stimulus, and that this should have been evident in the latency to approach stimuli. On the contrary, in the present experiment LE chicks showed a preference for approaching the face-like stimulus (and this effect did not involve the dependent variable latency of approach).

We propose an interpretation of this result based on another most salient feature of the right hemisphere's functional specialization. In fact, evidence already exists in the literature showing that the right hemisphere of different species is dominant not only as regards fear reactions, but also as regards social cognition. In particular some evidence suggests that recognition of conspecifics is a right hemisphere process (Andrew, Johnston, Robins and Rogers, 2004; Deng and Rogers, 2002; Kendrick, Atkins, Hinton, Heavens and Keverne, 1996; Peirce, Leigh and Kendrick, 2000; Sergent and Signoret, 1992; Vallortigara, 1992; Vallortigara and Andrew, 1991; 1994; Ventolini, Ferrero, Sponza, Della Chiesa, Zucca and Vallortigara, 2005; see Daisley, Mascalzoni, Rosa Salva, Rugani and Regolin, 2009 for a review on domestic chicks). For example, the ability to recognize familiar from unfamiliar conspecifcs appears to be a right hemisphere process in the domestic chick (Vallortigara, 1992; Vallortigara and Andrew, 1991; 1994; Andrew, Johnston, Robins and Rogers, 2004). The recognition of individual conspecifics is mainly processed using the right hemisphere also in sheep (Peirce, Leigh and Kendrick, 2000) and in humans (Sergent and Signoret, 1992). As regards actual face perception, human data from neuroimaging studies and from brain disorder patients show a right hemisphere dominance in face perception (De Renzi, Perani, Carlesimo, Silveri and Fazio, 1994; De Haan, 2001; Kanwisher, McDermott and Chun, 1997; Sergent and Signoret, 1992). A right hemisphere advantage in face perception has even been hypothesised for human babies (de Schonen and Mathivet, 1989). In particular, evidence is there in the literature of a right hemisphere dominance also for newborns' looking preferences for faces (Valenza, Simion, Macchi Cassia and Umiltà, 1996). Thus, LE chicks had in use the hemisphere which is dominant for social responses, including face perception. For this reason, in LE chicks one of the two opposite tendencies that they were experiencing, namely the social predisposition to approach face-like stimuli, was stronger than the other one and thus able to emerge.

Therefore, results obtained in the present experiment confirm that also in domestic chicks, like in other animal species and in human beings, the right hemisphere seems to be in charge of face perception and face preferences. To the best of our knowledge, in Experiment 11 we have obtained the first direct evidence of a right hemisphere dominance, demonstrated by the use of the monocular occlusion technique, in domestic chicks' face preferences. Nevertheless, this result is in line with previous evidence on right hemisphere dominance in face perception in other species and with evidence on right hemisphere dominance in individual recognition and social cognition in chicks (see above).

On this regard, however, it is also interesting to compare results observed in LE chicks in Experiment 11 with those of LE chicks in Experiment 9. In fact, it may seem puzzeling that the same group of chicks that in Experiment 9 displayed avoidance for the face-like stimulus, would show a preference for a similar face-like configuration in Experiment 11. In order to fully understand these results it is necessary to focus on the differences between the face-like stimulus used in Experiments 9 and 11 (see Figures 36 and 37). The main difference between the face-like stimulus in Experiment 9 and 11 is the direction of contrast polarity: in fact, only the face stimulus used in Experiment 11 presents the correct contrast polarity for a face. It is thus reasonable to assume that the face stimulus used in Experiment 11 could be much more effective in eliciting social preferences in chicks, with respect to that used in Experiment 9 (see also Experiments 1 and 6). This in turn could have determined a shift in the response of the right hemisfere, from a response based on its specialization for anti-preadtory fear reactions to a response based on its dominance for social cognition and face perception (see above). Indirect evidence in favour of this hypothesis can be found in the observation of the different dependent variables that resulted sensitive to LE chicks' preferences in Experiments 9 and 11. In Experiment 9, in line with the presence of a fear-related response, chicks' preference was evident as regards latencies to approach stimuli (a dependent variable often associated with anti-predatory responses). On the contrary, in Experiment 11, chicks' preference was evident in the first stimulus approached, a measure of social preferences (see also Experiments 1 and 5).

## General discussion of Experiments 6-11

Overall, from results obtained in Experiments 6-11 we can conclude that the direction of contrast polarity is an important factor in domestic chicks' face preferences, in line with evidence available in the literature on human adults and newborn babies (Gilad, Meng and Sinha, 2009; Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). In fact, in Experiment 6 we demonstrated that reversal of contrast polarity abolishes chicks' preference for a schematic face-like stimulus. Experiments 10 and 11 have also, indirectly, demonstrated that restoring the normal direction of contrast polarity expected for a face can restore the original tendency to approach face-like stimuli. Such results further confirm the presence of strong parallelisms between face-preferences in newborn babies and visually deprived domestic chicks (in line also with results of Experiment 5).

Thus, in domestic chicks as in human beings, a stimulus, in order to be perceived as face-like, needs not only to have a certain configuration of inner features, but also to have the correct luminance pattern expected for a face under natural top-lit illumination. In fact, some ordinal relationships between luminance of different face areas are remarkably constant when a face is illuminated from above (see Gilad, Meng and Sinha, 2009). That is to say, for example, that the cheeks and forehead of a human face are always going to appear lighter than the eye orbits, under natural top-lit illumination. Similarly, the dark black eyes and the shadow under the bill (or the bill itself) of a domestic chick are always going to appear darker than other areas of its face (see Figure 7). Such constant luminance relationships may be quite widespread among vertebrate species, due to constraints associated with overall face structure. Future studies may be devoted to the investigation of this issue in different social animals, in order to understand whether the effect we have demonstrated in chicks can be replicated also in other social species having a different face-structure.

Therefore, we belive that the results we have obtained confirm, in domestic chicks, the presence of domain-specific mechanisms evolved on the purpose of successfully identifying face-stimuli as they appear in the natural environment (in line with what ipothesised by Morton and Johnson, 1991; Johnson, 2005; Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005).

We interpret our results in line with what suggested for newborn babies (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). According to the interpretation proposed by Farroni and her colleagues, newborn babies would possess a spontaneous tendency to look at stimuli having the pattern of lighter and darker areas typical of a face (as it appears in natural environment). Due to the fact that the eye and mouth regions are recessed on a face, under natual top-lit illumination they appear to be darker than other parts of the face. As a consequence, face-like patterns where the elements within the face are lighter than the background do not elicit face preferences. We believe that this interpretation is particularly relevant, because it stresses the domain-specific nature of the face preferences observed in chicks and in human babies. In fact, the interpretation offered by Farroni and her colleagues (2005) allows to contrast predictions originated by a domain-specific account of newborns' face preferences with predictions originated by theories that explain face preferences as due to domain-general attentional biases, such as the up-down bias theory (Turati, Simion, Milani and Umiltà, 2002). According to the up-down bias theory, for example, there should be no difference in preferences observed with pair of stimuli that differ in contrast polarity, as long as they do not differ in the distribution of inner features. Thus, the results that we obtained in Experiments 6-11 are in line with those of Experiments 1-4, in that they show that chicks' face preferences are domain-specific in nature, and not influenced by the vertical asymmetry of inner face elements.

On a further level of explanation it is also possible to argument that our results (as well as the results obtained in newborns by Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005), are in line with the theory proposed by Gilad, Meng and Sinha (2009). Gilad and colleagues explain the poor performance that adults have in recognizing negative images of faces, as due to the destruction of a small set of stable 2D contrast polarity relationships. It seems that the presence of the normal polarity of contrast in the region surrounding the eyes (with the pupils and irises being darker than the sclera, the cheecks and the forehead) is the crucial factor to determine face recognition. Due to the fact that these ordinal relationships are remarkably constant, they are incorporated in the facial representation used for face recognition in adults and for face detection in chicks and babies.

Up to the present moment we have discussed similarities between results obtained in chicks and in human babies. However, Experiments 7-9 also revealed important differences between domestic chicks and human newborns. In fact, while in human babies the addition of a pupil-like blob within face features restored the original preference for the face-like stimulus, this very same manipulation determined in chicks an avoidance of the face-like configuration. The effect obtained in human babies has been explained as due to the fact that "… *the function of newborns' orientation bias is to establish eye contact, and human eyes are identified as dark spots within lighter areas*" (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005).

We belive that the eye-like appearance of the two upper inner features of the face-like stimulus is also at the basis of the avoidance effect that we observed in chicks, after adding the pupil-like blob to our stimuli. In fact, domestic chicks are innately scared by the presence of stimuli that resemble one pair of eyes (e.g. Gagliardi, Gallup and Boren, 1976; Gallup, Nash, Donegan and McClure, 1971; Gallup, Nash and Ellison, 1971; Rosa Salva, Regolin and Vallortigara, 2007; Scaife, 1976). This response is likely to be an anti-predatory mechanism evolved to detect stimuli associated with the presence of a predator attentive to the chick. Thus, the face like-stimuli employed in Experiments 7-9, probably elicited such an anti-predatory fear response in chicks, due to the fact that, thanks to the pupil-like blob, its two upper features resembled a pair of predatory eyes (see see Figure 5 and see discussions of Experiments 7-8).

Therefore, Experiments 7-9 confirm that features representing the eyes are crucial in determining chicks' responses to face-like stimuli, even though chicks' reactions to eye-like shapes can be opposite with respect to reactions displayed by newborn babies. Why should the presence of eye-like shapes affect in such a different fashion domestic chicks and human babies? The most likely explanation of such discrepant results refers to the differences between the ecologic niches of the two species. We are an atricial species. For this reason newborn babies depend completely on the presence and care of an adult caregiver. Thus, the capability to engage in a social exchange with his/her adult caregiver is crucial for a human newborn, whose looking preferences are likely to have evolved, among other things, also in order to identificate communicative partners and establish eye contact with them.

Moreover, due to the fact that human newborns are completely helpless and unable to defend themselves, it would be useless for them to be endowed with an innate avversion for stimuli that resemble potential predators: babies' only chance to survive to predators depends on their adult caregiver. On the contrary, domestic chickens are a precocious species, whose offsprings are able to move around in the environment (and to hide away from predators) from the very first days of life. Therefore, this species needs not only to be able to recognize appropriate social partners early after hatching, but needs also to possess some simple mechanism to detect the presence of potential predators attentive to the chick. Thus, a pair of eyes may elicit completely different responses fin the two species.

A final element of interest in our results is the presence of lateralization effects emerged in Experiments 9 and 11. It is now well known that brain asymmetries occur throughout the animal kingdom (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005). What was once considered a uniquely human characteristic, brain lateralization and its behavioural effects, has been found and studied in a wide range of species, including nonhuman primates (e.g. Fernandez-Carriba, Loeches, Morcillo and Hopkins, 2002), birds (e.g. Rogers, 1997), amphibians (Vallortigara, Rogers, Bisazza, Lippolis and Robins, 1998), fish (e.g. Sovrano, Rainoldi, Bisazza and Vallortigara, 1999) and invertebrates (Ades and Ramires, 2002; Letzkus, Boeddeker, Wood, Zhang and Srinivasan, 2007; Rogers and Vallortigara, 2008). In particular, domestic chicks are known to be lateralized in many different behaviours (Vallortigara, 1994).

With regard to the purpose of the present thesis, two aspects of the lateralization effects observed in Experiments 9 and 11 are of particular relevance. First of all, in Experiment 11 we have obtained the first direct evidence, demonstrated by the use of the monocular occlusion technique, of a right hemisphere dominance in domestic chicks' face preferences. In human beings (but also in animal species, see Kendrick, Atkins, Hinton, Heavens and Keverne, 1996; Peirce, Leigh and Kendrick, 2000) the right hemisphere seems to be in charge of face perception (De Renzi, Perani, Carlesimo, Silveri, Fazio, 1994; De Haan, 2001; Kanwisher, McDermott and Chun, 1997; Sergent and Signoret, 1992) (in line with its more general dominance for social cognition). In the human literature, this right hemisphere dominance has been considered as one of the hallmarks of specialized face processing in our species. Therefore results of Experiment 11 uncovered a further and important similarity between face preferences in human newborns (Valenza, Simion, Macchi Cassia and Umiltà, 1996; see also de Schonen and Mathivet, 1989) and domestic chicks.

Finally, it is worth noting that the direction of the lateralization effect observed in Experiments 9 and 11 was modulated by contrast polarity of test stimuli (see discussions of Experiments 9 and 11). This effect is a further proof that manipulations affecting contrast polarity can alter chicks' reactions to face like stimuli.

## Conclusions

It has long been debated as to whether face preferences found in newborns of some vertebrate species, and in general face perception abilities, are determined by domain-specific mechanisms. Moreover, the role of experience in determining such mechanisms is still a controversial issue (see "Introduction").

The results obtained in the experiments conducted for this thesis are consistent with the presence of a CONSPEC-like domain-specific mechanism for the detection of faces in visually naive domestic chicks (Morton and Johnson, 1991; Johnson, 2005). In the absence of any previous visual experience with faces, chicks showed a preference for stimuli presenting the triangular configuration of inner features typical of a face (Experiments 1 and 5), in line with the presence of an innate representation (CONSPEC) that directs the animals' attention toward stimuli whose internal features are arranged according to a face-like configuration. The fact that chicks' preferences were elicited both by schematic face-like stimuli and by faces of other species is a further element in line with the presence of a very broad representation of faces' appearance, as that theorized by the CONSPEC-CONLER model. These results confirm previous evidence obtained by studies that investigated chicks' preferences for artificial stimuli (such as a red box) and naturalistic stimuli (such as stuffed hens or polecats, Johnson, Bolhuis and Horn, 1985; Johnson and Horn, 1988). Results obtained here, in addition to confirming previous evidence, also provide original elements in favour of the presence of a CONSPEC-like face-specific detection device in chicks. We have investigated the role of three different perceptual properties in domestic chicks' face preferences. Neither vertical asymmetry of inner facial elements, nor spatial frequencies composing stimuli should have influenced chicks' face preferences, according to the model proposed by Johnson (Johnson and Morton, 1991; Johnson, 2005). In fact, both such properties were ruled out as explicative factors for chicks' face preferences (Experiments 1-5). On the contrary, Johnson theorized a crucial role of contrast polarity in face preferences (Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). Again, such a central role of contrast polarity was confirmed in chicks (Experiments 6 and 11). Therefore, Johnson's model, which is the most widely accepted explanation of face preferences in human babies, seems to apply also to domestic chicks, as already suggested by Johnson himself (Morton and Johnson, 1991; Johnson, 1992). Results obtained here are particularly relevant on this regard because in our experiments it was possible to confirm the presence of a CONSPEC-like social mechanism in chicks that never had any previous visual experience with faces (thus ruling out a confounding factor almost impossible to control for in newborns' studies).

Another important aspect of the results described in this thesis is the convergence between some relevant features of face preferences displayed by the newborns of two phylogenetically distant vertebrate species (visually naïve domestic chicks and newborn babies). In fact, in line with the evidence available for human newborns, chicks showed spontaneous preferences for faces. Chicks' preferential approach was elicited by both schematic and photographic stimuli, confirming data obtained for human babies' looking preferences (Experiments 1, 3-4 and 5; for data on human babies see Morton and Johnson, 1991; Macchi Cassia, Turati and Simion, 2004). Moreover, chicks' preferences were abolished by reversal of contrast polarity (Experiment 6, similar to what shown in newborns by Farroni, Johnson, Menon, Zulia, Faraguna and Csibra, 2005). A lateralization effect in favour of the right hemisphere was even obtained for chicks' face preferences (Experiment 11, in line with evidence of a dominant role of this same hemisphere for face perception oin human beings and other species, see the "Discussion" of Experiment 11). Finally, chicks' face preferences resulted also to be not species specific (Experiment 5), in line with the results of some recent studies showing that social preferences in human newborns and in other primates are not species-specific (Simion, Regolin and Bulf, 2008; Sugita, 2008).

In the social domain, evidence of common mechanisms in distant vertebrate species has already been obtained for biological motion detection, another crucial social ability, which is displayed by both newborn chicks and human babies (Vallortigara, Regolin and Marconato, 2005; Vallortigara and Regolin, 2006; Simion, Regolin and Bulf, 2008). With this result in mind, some have speculated on the existence of a life-form perceptual detector implemented within evolutionary ancient neural pathways (Johnson, 2006; Troje and Westhoff, 2006; for evidence of an animate being detection device in human adults see New, Cosmides and Tooby, 2007). Taken together with the results from this thesis, a consistent picture emerges about the presence of a primitive set of mechanisms for detecting other animals, which could involve independent mechanisms responding to biological motion and to faces. It is possible that other undiscovered biases exist and ensure preferential processing of other important aspects of conspecifics' appearance (or even of the appearance of any other animate creature encountered). For example, both newborn babies and visually-deprived chicks react to gaze direction (Farroni, Csibra, Simion and Johnson, 2002; Farroni, Pividori, Simion, Massaccesi and Johnson, 2004; Rosa Salva, Regolin and Vallortigara, 2007). However, it should be noted that sensitivity to eye direction may have evolved in chicks as an anti-predatory, rather than a social-affiliative, mechanism since recognizing where/what a predator is looking/seeing could be highly advantageous (see below, and see also the paragraph "Face perception in avian species").

However, many issues still remain to be addressed. It is still unclear whether the consistent behaviour observed in newborn babies and domestic chicks could be considered as a product of evolutionary conservation (homology of mechanisms inherited from a common ancestor) or convergent evolution (homoplasy of mechanisms evolved independently in different species in order to cope with similar selective pressures). Domestic chickens and human beings are phylogenetically very distant, but these two species could either share a common vertebrate neural system for detecting conspecifics, or have undergone convergent evolution for a common important function. Both are highly social species (e.g. Mench and Keeling, 2001; see also Daisley, Mascalzoni, Rosa-Salva, Rugani and Regolin, 2009), which have been exposed to selective pressures that could lead them to process faces in a privileged fashion and to spontaneously prefer faces early after birth. However, homology also remains a possibility, despite the phylogenetic distance between the two species. Other authors have already summarised evidence to support the existence of innate social-cognition mechanisms shared by mammals and birds (e.g. Baron-Cohen, 1994). On the other hand, according to Emery and Clayton (2004), the complex cognitive abilities that underly social cognition, which are shared by speicies so diverse such as primates and some avian species, have been evolved multiple times in phiologentically distant species in order to cope with similar socio-ecolgical problems. Further, homologies in the brain structures of mammals and birds are being increasingly recognized (e.g. Jarvis et al., 2005). As regards the presence of homologies in the hypothesised neural basis of face preferences, three areas have been hypothesised to be part of the human subcortical face-detection route (superior colliculus, pulvinar and amygdala, Johnson, 2005): all these three areas have homologues within the avian brain (optic tectum, nucleus rotundus, and amygdala, for reviews see Jarvis et al., 2005; Reiner, 2005; Reiner, Yamamoto and Karten, 2005; Bulter and Cotterill, 2006). It is also worth noting that the similar role played by subcortical visual brain structures of phylogenetically distant species (e.g. birds and mammals) in stimulus recognition has recently been discussed, particularly with regard to the recognition of conspecifics (Sewards and Sewards, 2002). Future comparative studies are required to definitively decide between continuity and convergence. For example, atricial birds (i.e. non-precocious birds which do not leave the nest independently in the first days of life) or non-social birds should present a similar pattern of face-preferences to that observed in the present study if continuity rather than convergence explains the present results.

Finally, if on the one hand the evidence described in this thesis shows remarkable parallels between face preferences displayed by domestic chicks and human babies (further validating the use of the domestic chick as an animal model for comparative studies with respect to newborn babies), on the other hand the differences emerged between the two species are also informative and should be analyzed.

The most striking difference between the behaviour of domestic chicks and human newborns regards the role of the vertical asymmetry of inner facial elements. The so called “up-down bias” has in fact a crucial role in human newborns’ face preferences, but does not seem to be relevant for chicks. Some possible reasons for such discrepant evidence have already been proposed in the “General discussion of Experiments 1-4”. We believe that, in a comparative perspective, the most interesting argumentation is that mechanisms underlying face preferences available to the two species could be different, due to the different needs that the two species encountered in their niches. Domestic chicks, being the offspring of a precocious species ready to move freely in the environment short after hatching and to imprint on the first salient object encountered, are probably in need of the ability to accurately discriminate biological objects with respect to inanimate ones. Chickens could thus have evolved a relatively "detailed" representation of the appearance of a face, as defined by its triangular arrangement of inner features, whereas human newborns would be endowed only with a general preference for top-heavy stimuli (sufficient, together with their sensitivity to contrast polarity, to select the parent's face among the common stimuli encountered in their environment) (see the "General discussion of Experiments 1-4").

Another important difference between domestic chicks and human babies emerged as regards their reaction to eye-like stimuli. In infants eyes and gaze are the most crucial parts of the face in order to determine face preferences: eyes appear to be an important social stimulus for newborn babies (e.g. see Easterbrook, Kisilevsky, Hains and Muir, 1999; Farroni, Csibra, Simion and Johnson, 2002; Farroni, Johnson, Menon, Zulian, Faraguna and Csibra, 2005; Farroni, Pividori, Simion, Massaccesi and Johnson, 2004). In line with that evidence, Experiments 3-4 demonstrated that inner features representing the eyes may actually be important also in chicks' face preferences. However, the eyes seem to represent a social stimulus for chicks only as long as they are inserted in an appropriate face-like configuration (e.g. a configuration having the correct contrast polarity for a face, as in Experiments 3-4, but not in Experiments 7-9). Another crucial factor in determining whether eyes would elicit a social or an anti-predatory response in chicks is the appearance of the eyes themselves. In fact, in chicks (but not in newborns, see Farroni, Johnson, Menon, Zulian, Faraguna and Csibra, 2005), an avoidance reaction is elicited by a pair of eyes that resemble the eyes of a potential predator (i.e. a pair of eyes having darker inner elements corresponding to the pupil or the iris contrasting with a lighter outer surface, corresponding to the iris or the sclera). The reason for such a different response to eye-like stimuli in the two species seems to be quite straight forward. First of all, human eyes present the configuration of darker and lighter concentric areas that elicits fear reactions in chicks (see also Rosa Salva, Regolin and Vallortigara, 2007). In fact, human beings are likely to be a potential predator also for the wild ancestors of domestic chickens, and therefore chickens are likely to have evolved innate fear reactions to human-like eyes. On the contrary, human newborns are of course spontaneously attracted to human eyes as a social stimulus. Moreover, besides human beings, in many other potential predators the eyes present the same distinctive luminance pattern characterised by a concentric organization of the two areas having different luminance (see Figure 5). Thus, domestic chicks have good reasons for being afraid of and avoid this kind of eye. On the contrary, a similar avoidance reaction in newborns would impair the development of appropriate social interactions between human babies and their adult caregivers. Finally, an avoidance reaction to predatory eyes would be useless for human infants. In fact, human newborns are completely helpless and unable to defend themselves or even to hide away from predators. Therefore, babies could not in any case benefit from an innate aversion for stimuli that resemble the eyes of potential predators.

However, it is important to remember that, despite the clear data in favour of the presence of anti-predatory fear reactions induced by eyes and eye-gaze in avian species (see the paragraph “Face perception in avian species”), some evidence for the presence of the ability to process eye-gaze in a social context exists also for avian species. For example, hand raised ravens (*Corvus corax*) are able to follow the gaze direction of a human being, starting from the first months of age (Bugnyar, Stowe and Heinrich, 2004; Schloegl, Kotrschal and Bugnyar, 2007). Moreover, in domestic chicks, previous experience with human gaze could alter the fear reaction normally induced in this species by the direct gaze of a potential predator (Rosa Salva, Regolin and Vallortigara, 2007). Future studies could be devoted to investigate how previous experience interacts with the spontaneous fear reaction induced by predator-like eyes in different avian species. It could be particularly interesting also to compare social species (like domestic chicks) with non-social species, to check whether the effect of experience with the gaze of a potential predator would be similar in both of them.

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