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SECTION V

Typical and atypical development of the social brain

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CHAPTER 10

The processing of social stimuli in early infancy: From faces to biological motion perception

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Abstract: The processing of social stimuli in early infancy: From faces to biological motion. There are several lines of evidence which suggests that, since birth, the human system detects social agents on the basis of at least two properties: the presence of a face and the way they move. This chapter reviews the infant research on the origin of brain specialization for social stimuli and on the role of innate mechanisms and perceptual experience in shaping the development of the social brain. Two lines of convergent evidence on face detection and biological motion detection will be presented to demonstrate the innate predispositions of the human system to detect social stimuli at birth. As for face detection, experiments will be presented to demonstrate that, by virtue of nonspecific attentional biases, a very coarse template of faces become active at birth. As for biological motion detection, studies will be presented to demonstrate that, since birth, the human system is able to detect social stimuli on the basis of their properties such as the presence of a semi-rigid motion named biological motion. Overall, the empirical evidence converge in supporting the notion that the human system begins life broadly tuned to detect social stimuli and that the progressive specialization will narrow the system for social stimuli as a function of experience.

Keywords: brain specialization; innate predispositions; face processing; biological motion; infancy.

Introduction

Detecting and discriminating humans from objects are critical for adaptive behavior. Many vertebrates orient toward or look longer at social agents. Newly hatched chicks attend to patterns similar to the head region of their caregivers (Morton and Johnson, 1991) and detect social agents on the basis of the way they move (Regolin et al., 2000). Similarly, monkeys manifest a preference for faces as compared to objects

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(Sugita, 2008). These findings support the idea of the existence of hard-wired mechanisms to detect social stimuli, which might be present in animals including humans (Johnson, 2007).

In effect, human adults are experts in processing social stimuli, such as faces, and evidence from behavioral, brain lesion, and neuroimaging studies suggests that, in adults, both face processing and biological motion perception involve specific processes carried out by dedicated brain areas (Allison et al., 2000; Farah et al., 2000; Kanwisher, 2000). Together, these findings support the hypothesis that a network of specific cortical circuits preferentially processes social information. This specialized network has been termed the "social brain" (e.g., Adolphs, 1999, 2003; Johnson et al., 2008) and has been extensively investigated in adults. However, the experience-dependent or experience-independent origin of such circuits is still a matter of dispute that developmental studies can help to solve.

Three different hypotheses have been proposed to explain brain specialization for social stimuli: the maturational, the skill learning, and the interactive specialization views (e.g., Johnson, 2001). The *maturational* view assumes that, through evolutionary pressure, specific parts of the brain and areas of the cortex have become dedicated to process social information. Some of the specific circuits to process social stimuli would be present and functioning at birth; in contrast, other circuits would become available through maturation later during development. The sequence of the maturational timetable would not be affected by experience.

The *skill-learning hypothesis* maintains that social stimuli are not different from other stimuli. Some circuits become specialized for social stimuli simply because adults become experts in processing them. The specialization would arise not because of the social nature of stimuli (i.e., domain specificity), but because of the expert-level discrimination for processing complex visual patterns, independently of the category to which the stimuli belong (i.e., process specificity) (e.g., Tarr and Gauthier, 2000).

The interactive specialization view emphasizes the importance of the initial biases to "bootstrap" later developing systems, and the notion of partial functioning of neural pathways which, interacting with the environment, shapes the subsequent functional and structural development. Starting from a constructivist viewpoint, this third hypothesis maintains that the structural and functional changes in regions of the cortex codevelop as a function of the interaction with the environment (Johnson, 2000) and that the timing of events plays a critical role in developmental trajectories. The specialization of the cognitive system cannot be ascribed to the prespecification of a particular region of the cortex, but to a particular sequence of interactions between pre- and postnatal environment and cortical circuits, resulting in successive reorganizations of the cortical circuits themselves (de Schonen, 2002). The postnatal functional brain development, at least within the cerebral cortex, involves a process of organizing patterns of interregional interactions (Johnson, 2002). The specific properties of a brain region are partly determined by its pattern of connectivity to other regions and to their pattern of activity. Cognitive specialization is, therefore, an activity-dependent and an experience-dependent process, strictly linked to the exposure to certain experiences occurring over a particular period of time, called a critical or sensitive period (Greenough and Black, 1992). Experience appears to play a prominent role in recruiting the cortical areas potentially suited to be activated by certain stimuli. The activation of these cortical and functional networks, in turn, leads to a process of a progressive specialization, which emerges if the critical type of input is provided within the sensitive time window and, therefore, is activity expectant (Nelson, 2001, 2003).

In line with the neoconstructivist approach, the cognitive activity is seen as emerging gradually from the interaction between innate constraints and the structure of the input provided by the species-typical environment (e.g., de Schonen, 2002; Elman et al., 1996). The specific computations of the cortical regions are the outcome of a continuous process of interaction between the innate predispositions and experience with the specific environment, which progressively leads to an increasing functional specialization of neural circuits (Bates and Elman, 1993; Johnson, 1997). Consequently, brain specialization, domain specificity, and cognitive modules, rather than being assumed as genetically prespecified, are considered to emerge epigenetically and developmentally through the interaction with postnatal environment.

Evolution has prespecified many innate biological constraints on development that are domain-general mechanisms becoming "domain specific" at later stages. During this process, the same general mechanisms have been used repeatedly to process a certain class of stimuli and, in so doing, they become specific. Some apparent constraints contribute to the development of new structures and new modes of functioning (Karmiloff-Smith, 1992) and provide starting points that channel the subsequent perceptual and cognitive development (e.g., Turkewitz and Kenny, 1982). The notion of innate constraints is described as architectural, computational, and temporal biases that shape information processing, limiting the types of input to be selected and constraining the computations on the input. Benefits from these biases consist in selectively focusing the cognitive system toward certain aspects of the surrounding environment or facilitating processing of certain inputs, thus strengthening learning of some categories of stimuli rather than others, and, consequently, tuning the system to become specialized.

This chapter will examine the emergence of the specialized cognitive system devoted to processing social stimuli and how innate mechanisms and perceptual experience contribute to the development of the social brain. To this end, we will focus on the evidence on infants' abilities from birth for processing social stimuli on the basis of the presence of a face (i.e., face detection) and of the way they move (biological motion detection). Two lines of convergent evidence will be presented to demonstrate the innate predispositions of the human system to detect social stimuli at birth and how the prewired perceptual constraints and attentional biases interact with experience to guide and shape the emerging of a specialized system to process social stimuli.

Mechanisms to detect faces at birth

From a very young age, humans display an impressive ability to process information embedded in the face, such as identity (Pascalis and de Schonen, 1994), emotional expression (Farroni et al., 2007), and direction of gaze (Farroni et al., 2000a,b; Vecera and Johnson, 1995). Face detection, instead, refers to the ability to decide whether or not a given stimulus is a face. Results show that, despite their lack of experience with faces, newborns prefer to orient to and to look longer at face configurations, rather than at other, equally complex, nonface stimuli (Goren et al., 1975; Johnson and Morton, 1991; Macchi Cassia et al., 2004; Valenza et al., 1996).

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Two interpretations were proposed to account for newborns' face preference. Some researchers proposed that a subcortical visuomotor system, named "Conspec", is present at birth and biases newborns to orient toward stimuli that contain the geometry of a face (i.e., two eyes above a nose and a mouth; Johnson and Morton, 1991; Morton and Johnson, 1991). A two-process model was hypothesized in which Conspec is present at birth and its primary function is to ascertain that facial input is maximized during the first 2 months of life, before a second cortical system, named Conlern comes up. In fact, at approximately 2 months of age, Conspec is replaced with or set by Conlern, an experientially based face-processing mechanism. An alternative and complementary hypothesis might be that both Conspec and Conlern mechanisms are present at birth and that the visual cortex also heavily contributes from birth to develop a face recognition system (Acerra et al., 2002). From previous research, specific visual cortical networks start to function over the first 6 months of life—first for discrimination of orientation, then directional movement and then binocular disparity (e.g., Atkinson, 1984, 2000). These cortical networks tuned for discrimination of specific visual attributes allow the cortex to take over executive control from subcortical networks operating at birth. One example is the directional movement system of optokinetic nystagmus (OKN) which is operational in newborns (a functional subcortical stabilizing system), which becomes superseded by a cortical directional motion system at around 8 weeks of age when this cortical system starts to function (Atkinson and Braddick, 1981). The model of face detection has been recently updated (Johnson, 2005) in a way similar to this, in that a primitive subcortical system operating at birth, interacts with areas in the cortex necessary for face recognition postnatally, which then takes over to be part of the adult social network for face discrimination. The model posits the existence of a low-spatial frequency (LSF) face configuration detector, provided by evolutionary pressure active throughout the life span (Tomalski et al., 2009). In this model, face detection would be supported by a "quick and dirty" subcortical route sensitive to a raised surface with darker areas corresponding to the locations of eyes. This subcortical pathway might be important to trigger the network of cortical regions that makes up the adult social brain. Specialization of the face cortical circuits might then emerge due to a combination of factors, including subcortical mechanisms that function to guide infants' visual attention to faces during the first weeks of life, biasing the input to the developing cortical system, increasing experience with faces, and increasing demands to process faces as infants develop. Importantly, it has been proposed that impairments to the subcortical route result in specific types of atypical development, such as autism. Specifically, if the subcortical face-processing route is important for the development of the adult social brain network, then disruption of this pathway by congenital factors could have important negative consequences for the social brain network as a whole (Johnson, 2005).

Recently, behavioral work with newborns has questioned the assumption of the existence of a specific face-detecting mechanism, suggesting that face preference at birth might be explained on the basis of the additive effect of general perceptual properties present in a face as well as in other visual stimuli. According to this hypothesis, newborn preference for faces may be the result of the match between perceptual and structural properties present in a face and the constraints of the newborn's sensory system (Simion et al., 2001).

This alternative hypothesis suggests that the presence at birth of non-face-specific attentional biases is sufficient to produce the emergence of the functional and neural specialization for faces observed later during development. The adult face-processing system appears thus capable of bootstrapping from minimal information, not requiring highly specific predispositions. This view is consistent with the linear system model (LSM) proposed by Banks and Salapatek (1981) accounting for newborns' visual preferences in terms of the match between the characteristics of the newborns visual system and the psychophysical properties of the stimuli as described by both the low level properties (i.e., contrast and spatial frequency content described by the amplitude spectrum) and higher level variables (i.e., the structural properties of a stimulus described by the phase spectrum) according to the Fourier transform (see Acerra et al., 2002 for a computational model of face processing).

Based on the alternative view, face preference at birth would be the result of the cumulative effect of a set of nonspecific constraints that stem from the general characteristics of the immature visual system and a collection of general structural properties that attracts newborns' attention. This claim derives mainly from the demonstration that, in addition to facedness, newborns manifest spontaneous preference for other structural properties of visual stimuli. For example, when horizontal gratings were paired with vertical gratings, newborns preferred the horizontal ones (i.e., Farroni et al., 2000a,b; Slater et al., 1985). Because the patterns were equated for quantity of energy (LSFs), one can assume that orientation, which is a structural property of the stimulus, was the crucial factor in determining the preference for horizontal gratings. Therefore, facedness might be preferred because of the additive effect of a collection of structural and perceptual properties. In effect, faces are symmetrical along the vertical axis, present more patterning in the upper compared to the lower half and have rounded rather than straight edges. The possibility exists that some if not all of these properties play a role in promoting the newborns' attentional response toward face-like stimuli and veridical face images. Data from our lab showed that at least two nonspecific structural properties not only are preferred at birth when embedded in nonface geometric configurations (Macchi Cassia et al., 2002, 2008; Simion et al., 2002) but also play a major role in determining newborns' preference for faces (Macchi Cassia et al., 2004; Turati et al., 2002).

A first property, termed up-down asymmetry (or top-heaviness), is defined by the presence of higher stimulus density in the upper than in the lower part of the configuration (Macchi Cassia et al., 2004; Simion et al., 2002; Turati et al., 2002). It has been demonstrated that newborns orient their gaze more frequently to, and look longer at, geometrical stimuli with more elements in the upper part when contrasted with the upside-down version of them (Simion et al., 2002; Fig. 1).

The same results were replicated with face-like stimuli (Turati et al., 2002) and with real faces (Macchi Cassia et al., 2004) in which the geometry of the face was disrupted. Indeed, Turati et al. (2002) demonstrated that an upright stimulus with two blobs randomly located in the upper part, and only one blob in the lower, was always preferred over the upside-down stimulus, thus showing that the correct face disposition of the inner elements is not necessary to induce a preference (Fig. 2a). Further, when face-like and non-face-like pattern are equated for the number of elements in the upper part of the configuration newborns' face preference disappears (Turati et al., 2002; Fig. 2b). Even more interesting is the result showing a visual preference for a non-face-like arrangement of elements located in the upper portion of the stimulus over a face-like arrangement positioned in the lower portion of the pattern (Turati et al., 2002; Fig. 2c). These results strongly suggested that when facedness and up-down asymmetry were directly contrasted, the upper position of the elements within the contour (i.e., up-down asymmetry), rather than the spatial relations among the blobs (i.e., facedness), proved to be the crucial factor in determining newborns' preference.

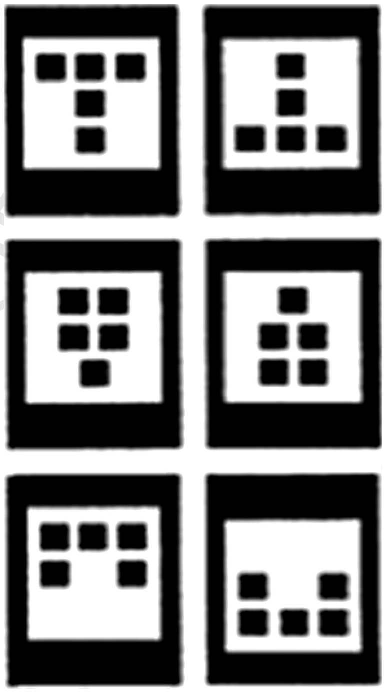

Fig. 1. Stimuli used to investigate the "up-down asymmetry" with geometrical stimuli (Simion et al., 2002).

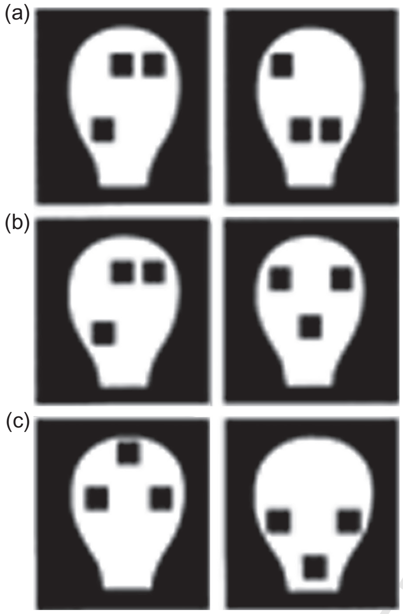

Fig. 2. Face-like stimuli employed to demonstrate the “up-down asymmetry” in newborns (Turati et al., 2002).

The same conclusion was supported by similar results obtained using real faces and manipulating the position of the inner features within the face (Macchi Cassia et al., 2004). Newborns preferred a scrambled face with more features in the upper part (Fig. 3a) and did not manifest any visual preference between a real face and a scrambled face equated for the number of features appearing in the upper and lower halves (Fig. 3b). Finally, when a veridical face was contrasted with a scrambled face with more elements in the upper part, newborns manifested a preference for the scrambled face (Simion et al., 2006).

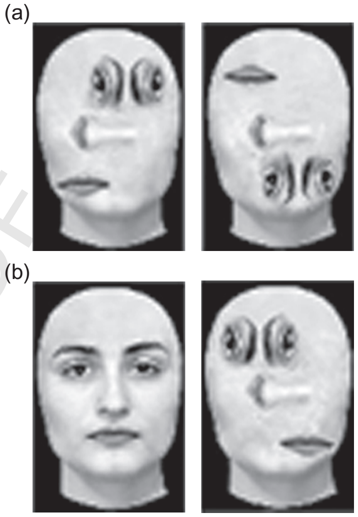

Fig. 3. Real and scrambled faces employed by Macchi Cassia et al. (2004).

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These findings suggest that it may be unnecessary to assume the existence at birth of an experience-independent “face detector” sensitive to face geometry. Rather, newborns’ face preference likely results from a general attentional proclivity toward top-heavy stimuli, which may in turn derive from endogenous constraints of the newborns’ visual system. Specifically, Simion et al. (2002) suggested that a possible explanation might derive from the existence of an upper versus lower visual field difference in visual sensitivity, similar to that already observed in adults (e.g., Heywood and Churcher, 1980; Rizzolatti et al., 1987). Newborns may find top-heavy patterns more easily detectable than other stimuli because of the existence at birth of an upper visual field advantage in visual sensitivity. This advantage is supposed to be due to the fact that a major role in visual exploration of the upper visual field is played by the superior colliculus (Sprague et al., 1973), which is supposed to affect consistently newborns’ visual behavior (Atkinson et al., 1992).

The second nonspecific property that can explain face preference at birth is the presence of a congruent or corresponding relationship between the shape and orientation of the contour and the spatial disposition of the included features. Faces can be described as a congruent configuration, as they display a greater number of features (the eyes) in the wider, upper portion of the face outline and only one feature (the mouth) in the narrower part. The hypothesis that congruent visual configurations may be preferred at birth over noncongruent patterns appears reasonable in light of two lines of evidence. First, newborns are highly sensitive to configural–holistic properties emerging from the interrelations between the component parts of the stimuli. For instance, they can perceive the invariance of the spatial relationship between single features, which vary in their absolute position within an array (Antell et al., 1985). Also, newborns are able to group separate sets of elements according to Gestalt principles (Farroni et al., 2000a,b), and they find configural and global cues in hierarchical patterns more easily detectable than featural and local information (Macchi Cassia et al., 2002). Second, based on Gestalt theories of visual perception (Palmer, 1991), in comparison to noncongruent configurations, congruent configurations provide a better fit for the criteria of figural simplicity and regularity that render visual patterns more easily and economically processed and represented by the human perceptual system. Because newborns have been shown to perceive and organize visual arrays according to Gestalt principles, such as lightness similarity (Farroni et al., 2000a,b) and common motion (Valenza and Bulf, 2007), it seems reasonable to hypothesize that newborns may be sensitive to other stimulus dimensions that contribute to figural goodness, such as symmetry, repetition, and regularity. Each of these dimensions is maximally present in congruent visual configurations. Evidence revealed that when congruent and noncongruent nonface configurations were compared (using both triangles and trapezoids), a reliable tendency to prefer the congruent pattern was observed in newborns. A top-heavy congruent stimulus was preferred over a top-heavy noncongruent stimulus, thus indicating that the congruency and top-heavy properties have an additive effect on newborns' preferences (Macchi Cassia et al., 2008; Fig. 4).

Further evidence that highlighted the effect of up-down asymmetry and congruency comes from a recent study that demonstrated that newborns, in the absence of either featural information or second-order relational information (which refers to fine spatial relations between features, such as the distance between the eyes), manifest a preference for an upright Mooney face[1] when compared to a Mooney-like object equated for the number of elements in the upper part (Leo and Simion, 2009). This preference demonstrates that newborns both organize the patches of intense light and shadow in a face Gestalt representation and perceive the difference between the two configurations equated for the number of elements in the upper part and prefer the one where a congruent disposition of the elements is present.

Fig. 4. Stimuli employed to demonstrate that a top-heavy congruent stimulus was preferred over a top-heavy noncongruent stimulus (Macchi Cassia et al., 2008).

Overall, the results obtained in our lab support the idea that face preference is in fact a preference for some general perceptual and structural properties that faces share with other visual stimuli.

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[1] Mooney stimuli are extremely high-contrast photographs in which the face is formed only from white lit surfaces and black unlit shadows, and the perception of individual local features has been degraded by transforming all luminance values to black or white (e.g., Mondloch et al., 2003).

To summarize, the two hypotheses interpreting newborns' face preference are not mutually exclusive. In fact, even if they are not in agreement about the nature of the mechanisms underlying face preference at birth (i.e., domain-specific mechanisms, Johnson, 2005, and domain-general mechanisms, Simion et al., 2001), both hypotheses concur about the function of the mechanisms that ensure that newborns' attention is triggered by faces, and the resulting behavior, that is the preference for schematic and real faces. In other words, the mechanisms that drive face preference at birth are domain relevant, because they ensure the broadly tuned human system to become specialized, allowing newborns to successfully select faces among other non-face-like stimuli within their species-typical environment.

Face representation in the first months of life and the role of visual experience

The evidence on the existence of general mechanisms for face detection at birth seems to support the hypothesis of a face-representation system that changes over development and of a face space (i.e., a multidimensional space in which each individual face is coded as a point in a continuum where the average face lies at the center of the space, Valentine, 1991) that narrows over time, as proposed by Nelson (2001, 2003). According to this view, infants begin life with general mechanisms dedicated to processing faces as well as other stimuli that subsequently become "tuned" to human faces as a direct consequence of the extensive experience with this stimulus category provided by the species-typical environment within the first months of life (Scott et al., 2007). The unspecified face representation present at birth subsequently becomes finely tuned as a function of the incoming experience and of the facial input received.

This concept of a face representation is best understood within the framework of the multidimensional face space model proposed by Valentine (1991). This norm-based coding model suggests that faces are encoded as vectors according to their deviation from a prototypical average of the face space. As proposed by Nelson (2001), this face prototype is broadly tuned at birth and the dimensions that this prototype encodes may differ both qualitatively and quantitatively in infants compared with adults.

Pascalis et al. (2005) suggested that "a good way to think about the development or formation of a face prototype is based on the experience or kinds of faces one encounters. For example, if this prototype is thought of as a continuum of all incoming faces, then the more a face deviates from the prototype (other-race and other-species faces), the less this face is easily discriminated, compared with faces that are more similar to the prototype. Importantly, the development of the face prototype is likely influenced by a number of factors, including exposure time (number of faces seen), dynamic and emotionally salient information provided within the face and changes in the categorization of individuation of people. Combined, these experiences gradually lead to the face prototype becoming more specific" (p. 5298).

Early in life, infants possess a remarkable ability to discriminate among and between a large corpus of different faces, such as faces from an unfamiliar species or an unfamiliar race. With experience, the infant's face-representation system becomes more precise and increasingly restricted to faces with which infants are most familiar. This, in turn, results in the development of expertise, in which the ability to discriminate between faces that one has not been exposed to (or has had less exposure to) is not as good as discrimination between faces which one has experienced. This phenomenon is called "perceptual narrowing" (Lewkowicz and Ghazanfar, 2006; Nelson, 2001). A significant demonstration of perceptual narrowing and of the importance of early visual experience has recently been observed in animals by Sugita (2008). In this study, infant Japanese macaques were separated from their mothers at birth and reared by human caregivers for 6–24 months. During this period, the monkeys had no interaction with other monkeys or with other humans. In fact, the monkeys were prevented from seeing any faces: human caregivers wore masks whenever interacting with the monkeys. When tested using a preferential looking paradigm during the deprivation period, all monkeys showed a preference for both monkey and human faces over objects. But when human and monkey faces were presented simultaneously, monkeys did not exhibit a preference for either category of face. After the deprivation period, the infant monkeys were exposed for the first time to either human faces or monkey faces. Interestingly, when monkeys were tested a month after the deprivation period, their preferences had altered. In fact, they exhibit a preference for facial features to which they were exposed. Monkeys that were exposed to human faces showed a preference for human faces. In contrast, monkeys that were exposed to monkey faces manifested a preference for monkey faces. These results seem consistent with the hypothesis of the existence of a broadly tuned face representation at birth as well as an apparent sensitive period during which a broad but flexible face prototype develops into a concrete one for efficient detection of familiar faces.

Importantly, in line with these results, unpublished evidence from our lab demonstrated that newborns did not manifest any visual preference for a human face when contrasted with a monkey face, corroborating the idea that at birth face representation is largely unspecified (Fig. 5). Altogether, this pattern of results suggests that infants may have the ability to process a broad range of face types. With increased experience with certain types of faces and the lack of contact with other types of faces, perceptual narrowing takes place that leads the human system to increase the discriminatory abilities for the highly experienced faces and to decrease the ability to discriminate the infrequently experienced faces.

Fig. 5. Example of stimuli used to demonstrate that face representation at birth is unspecified (unpublished data from our lab).

According to Nelson's hypothesis, the face-processing system should become specific to human faces around or soon after 3 months, as a function of the faces seen in the visual environment (de Schonen and Mathivet, 1989; Nelson, 2001).

An example of how the social environment influences the tuning of face processing during the first months of life is the so-called other-gender effect. It has been demonstrated that 3-month-old infants prefer to look at female faces when paired with male faces and this preference was interpreted as a gender bias of the face prototype toward the primary caregiver (Quinn et al., 2002). Another example is the well-known "other-race effect" (ORE), in which adults find it easier to differentiate faces from their own ethnic group (Meissner and Brigham, 2001).

It has been demonstrated that selectivity based on ethnic facial differences emerges at the same age, with 3-month-old infants preferring to look at faces from their own group, as opposed to faces from other ethnic groups (Bar-Haim et al., 2006; Kelly et al., 2005). The lack of preference for either own- or other-race faces in newborns indicates that the infant's face representation may be "ethnically unspecified" at birth but is subsequently shaped according to the ethnicity of faces viewed within the visual environment (Kelly et al., 2005). A final example of the importance of early experience is the "other-species effect": 6-month-old infants are able to discriminate between both human and monkey faces,

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but the ability to discriminate monkey faces has diminished by 9 months of age (Pascalis et al., 2002).

The neuropsychological equivalent of this process of perceptual narrowing would be an increase in the selectivity and localization of the cortical circuits involved in face processing (Johnson, 2000). Over time, these circuits would pass from being activated by a broader range of stimuli to responding to only certain kinds of stimuli, thus giving rise to a more localized and specialized neural response. Note that this recently proposed model of face-processing development differs from that previously proposed by Johnson and Morton (1991) in that it assumes that general, rather than specific, initial input is sufficient to set the stage for the development of the face-processing system into its adult-like, specialized form. Indeed, some recent neuropsychological studies that measured event-related potential (ERP; Halit et al., 2003) or performed positron emission tomography (PET) scans (Tzourio-Mazoyer et al., 2002) suggested that, by 2–3 months of age, there are the first signs of cortical specialization for faces.

Based on the evidence of face-processing specialization within the first months of life, we conducted a series of behavioral studies to verify whether the same general biases that induce face preference at birth still operate and explain face preference 3 months later. More specifically, we tested whether the general structural properties such as up-down asymmetry that induces face preference at birth still operate at 3 months of age when a certain degree of cortical specialization for faces begins to emerge.

A first experiment conducted in our lab was clear in demonstrating that upright natural faces are still preferred and this result confirms the presence of the “inversion effect” at 3 months of age (Turati et al., 2005). This preference for the upright face was present not only when the face was contrasted with an inverted face, which has fewer elements than the face in the upper part, but also when it was contrasted with a scrambled face equated for the number of elements in the upper half (Macchi Cassia et al., 2006; Turati et al., 2005). Crucially, when an image of an upright face was presented together with a top-heavy scrambled face with a greater number of elements in the upper part of the configuration, 3 month olds still manifest a preference for the face (Simion et al., 2006). Altogether, these results showed that 3-month-old infants always prefer the real face, demonstrating that at this age, the up-down asymmetry in the distribution of the inner features can no longer be considered as a crucial factor able to induce infants’ preference for a face. Such pattern of evidence differs from that observed at birth, where faces are no longer preferred if they are paired with configurations equated with up-down asymmetry (Macchi Cassia et al., 2004; Turati et al., 2002).

To summarize, in our view, at birth, face preference seems to depend on the existence of general biases that orient newborns’ attention toward certain structural properties that faces share with other complex visual stimuli (Simion et al., 2001, 2002; Turati et al., 2002). In contrast, at 3 months of age, the face preference appears to be the product of more specific mechanisms that respond more selectively to those perceptual characteristics that distinguish faces from other stimulus categories. These data suggest the existence of different mechanisms that underlie face preference at birth and in 3-month-old infants. In addition, the developmental data reported here of a lack of preference between human face and monkey face both in humans and in monkeys has provided further evidence in support of an unspecified face representation at birth, which is shaped by the faces observed within the visual environment during the initial months of development, according to the idea of perceptual narrowing (Nelson, 2001). This is line with an experience-expectant perspective (Nelson, 2003) that highlights the importance of both general constraints of the human visuoperceptual system and exposure to certain experiences shortly after birth to drive the system to become functionally specialized to process faces in the first months of life.

Biological motion: Introduction

The data reviewed up to now converge in demonstrating that many vertebrate species, including humans, manifest a preference to select faces among other non-face-like stimuli. This perceptual bias toward faces provides high exposure to some important sensory information about conspecifics. However, detection and recognition of human beings among nonliving objects in the visual environment may be based not only on faces.

According to the Human First Hypothesis proposed by Bonatti et al. (2002), the face recognition system might be subordinate to a more general "human identification system" that can be triggered by different properties present in conspecifics, such as having a specific body schema or the presence of a specific body motion. In the same vein, some authors have hypothesized the existence of a "life detector," a mechanism that serves as a general detection system for terrestrial animals and is sensitive to the most informative features of vertebrate animal motion (Troje and Westhoff, 2006).

Interestingly, perception of faces, body and body motion seem to involve, in the adult human system, the activation of contiguous and dedicated brain areas (Allison et al., 2000). Whereas the origin of brain specialization for faces has been extensively investigated, the presence of an innate predisposition to detect social agents on the basis of the peculiarity of their motion has been scarcely investigated. In the following section, we will review the available evidence on the presence of an innate predisposition to detect social stimuli on the basis of the way they move.

Mechanisms underlying biological motion detection

Many adaptive responses to natural objects depend on the way such objects move. The way terrestrial vertebrates move is one of their most salient features. When a vertebrate moves, its limbs and torso undergo a specific pattern of motion constrained by the rigid skeletal structure supporting the body. Spatial relation among some body parts are continuously changing, whereas spatial relation between other parts, representing connected joints, remains invariant.

The human system is sensitive to the peculiarities of this kind of motion as a dozen point-lights placed on the main joints of a walking person is sufficient to convey the impression of someone engaged in a coordinated activity. The perception induced by this pattern of motion, namely biological motion, and the typical display used for its investigation, the point-light animation, was first described by Johansson (1973). Dynamic point-light displays are experimental tools to separate information concerning motion from other perceptual cues deriving from the body of the moving animal.

To adult viewers, point-light displays are easily recognizable and need as little as 100 ms to identify a point-light human walker, while 400 ms are enough to recognize the kind of action represented (Johansson, 1976). Also several animal species are able to discriminate and to respond to point-light displays (Omori and Watanabe, 1996; Regolin et al., 2000).

Moreover, to the human observer, such biological motion provides an important source of social information allowing adult observers to attribute socially relevant features, such as gender (Barclay et al., 1978; Kozlowski and Cutting, 1977), emotions (Dittrich et al., 1996; Pollick et al., 2001), actions (Dittrich, 1993), and intentions (Blakemore and Decety, 2001) to individuals. The impressive ability to organize individual dots in the biological motion display into a coherent, articulated shape of a human figure (e.g., Bertenthal and Pinto, 1994) suggests that the visual system rapidly carries out a very complex structure-from-motion analysis from the biological motion animations. This process may rely on the extraction of configural invariants from the relative motion of the elements in the sequence (Bertenthal et al., 1984) and on a process of global analysis probably driven by stored representation of familiar forms (Bertenthal and Pinto, 1994). According to this view, experience of forms and events is claimed to be necessary and the process is considered highly experience dependent.

Similarly to faces, detection and recognition of a point-light walking person are disrupted when the display is turned upside down (Pavlova and Sokolov, 2000; Sumi, 1984). An explanation that has been proposed maintains that inversion impairs the configural processing of the familiar shape (Bertenthal and Pinto, 1994). However, prior knowledge concerning display inversion is not sufficient for recognition of inverted biological motion displays. Also when the human body walking-on-hands was represented instead of walking on foot, either inverted or upright, subjects were less accurate at detecting walking-on-hands when the display was turned upside down rather than when it was upright, so that the orientation of gravity and not form seems crucial for recognition (Shipley, 2003). Overall, a perceptual rather than knowledge-based origin for the inversion effect is the most reasonable explanation for these data.

Recent results support the hypothesis that the perception of biological motion is not completely explained by form extraction. It has been recently shown that the detection of animacy and the discrimination of walking direction in biological motion displays might be conveyed by local motion cues, such as those provided by the specific signature of the ballistic motion of the feet of an animal in locomotion (Chang and Troje, 2008; Troje and Westhoff, 2006). Even when presented with spatially scrambled biological motion displays of humans or animals, which do not contain any structural information, adults correctly judge the direction in which a walker is facing, reporting to see a living being even if no animal species can be identified in such displays. However, when either the display or parts of it were inverted, participants' direction judgment was correct as long as the dots associated with the motion of legs remained intact (Troje and Westhoff, 2006). Thus, some motion cues, based on the dynamic of movement constrained by the direction of the force of gravity acting on the local motion, seem to be partially separate from configural information and independent from the nature of the form used to produce the stimulus.

It has been recently proposed that the sensitivity to biological motion is based on an innate predisposition to orient to and preferentially process motion information about living creatures (Johnson, 2006; Troje and Westhoff, 2006). Such an inborn life detection mechanism could constitute a primitive and basic mechanism, shared by vertebrates, driven by non-species-specific motion cues. This life detection system should be distinct from an acquired mechanism responsible for global shape processing that is required for more specific identification of an agent and its action (Chang and Troje, 2009). It has been proposed to extend the Morton and Johnson (1991) model of the epigenetic mechanisms underlying the development of face perception (Conspec and Conlern) to biological motion perception (Chang and Troje, 2009). The authors characterized Conspec as driven by dynamic features of local motion, such as those provided by the specific signature of the ballistic motion of the feet of an animal in locomotion (which are independent from global aspects of the stimulus). In contrast, an individually acquired global processing system (Conlern) should be responsible for the use of global cues to retrieve specific information about conspecifics. According to this hypothesis, the local motion would drive a mechanism that is available early, evolutionarily ancient and possibly innate (Chang and Troje 2009; Johnson, 2006; Troje and Westhoff, 2006). In contrast, an individually acquired global processing system would be responsible for the sensitivity to global configurations.

The origin of the sensitivity to biological motion

Given the adaptive significance of detecting biological motion, the hypothesis about an innate predisposition to extract the most informative features of biological motion is not surprising.

The issue concerning the experience-independent origin of the sensitivity to biological motion originates with Johansson (1976), who proposed that the perception of biological motion was an intrinsic capacity of the visual system. However, this hypothesis was never tested with human newborns until recently.

The hypothesis that sensitivity to biological is present early in human development was first supported with infant studies by Fox and McDaniel (1982). In this study, the ability to process and respond to biological motion stimuli was demonstrated in 4- and 6-month-old infants as they preferred to look longer to a point-light display depicting a walking person, compared to an array of elements moving in a random fashion. Moreover, infants preferentially looked at the canonical walking display rather than the same stimulus upside down. At 5 months of age, infants discriminate a human point-light display walker from the same stimulus with scrambled spatial relationships (Bertenthal et al., 1984) or with perturbed local rigidity between some joints (Bertenthal et al., 1987), suggesting that the sensitivity to motion-carried configural information emerges early in life. These results raised the possibility that the mechanisms subserving the perception of biological motion may at least in part, be experience-independent rather than acquired through experience. However, studies on infants were not able to unequivocally address the issue concerning the origin (innate or experience dependent) of the processes involved in the perception of biological motion in humans, because results with infants could always be accounted for by either maturational (innate) or learning mechanisms.

The first convincing evidence of an inborn ability to detect and specifically respond to biological motion came from nonhuman animal species. Imprinting procedure revealed that newly hatched chicks, tested prior to any visual experience, are able to discriminate biological motion displays from point-light displays depicting a random motion or the rotating motion of a solid object (Regolin et al., 2000). Moreover, visually inexperienced chicks were able to discriminate a point-light display representing a walking hen from the scrambled version of the same stimulus, revealing that chicks are sensitive to some configural information emerging from the relative motion of the elements in the display. Moreover, at their first exposure to point-light displays, chicks preferentially approached biological motion compared to nonbiological motion stimuli (Vallortigara et al., 2005). This spontaneous preference emerged in chicks irrespective of the species of animals used to produce the stimulus. In fact, chicks did not show any preference for the walking hen as compared to sequences representing a walking cat or even to a scrambled biological motion, suggesting a non-species-specific sensitivity to biological motion patterns. These findings are consistent with the idea of an evolutionarily ancient neural mechanism for detecting other legged vertebrates, and they join a growing body of evidence that specific neural systems are activated by the perception of biological motion in mammals, including man (e.g., Grossman et al., 2000).

The hypothesis that an inborn predisposition to orient to and preferentially process biological motion is present in humans, as well as in other vertebrate species, has been addressed by recent studies on 2-day-old babies. The same animations used to test the newborn chicks in previous studies were used with newborns, because previous comparative studies suggest that a general mechanism is at work, which should not be based on species-specific cues. Moreover, the use of hen-walking animations rather than human-walker animations ruled out the possibility that newborns may have had any previous experience with the kind of motion depicted in the stimuli used.

Results from our lab demonstrated that, at their first exposure, 2-day-old babies preferred biological motion over random motion point-light displays (Simion et al., 2008). In addition, newborns manifest a preference for the upright point-light display depicting a walking hen as compared to the same display upside down.

The authors explain these results as due to an inborn sensitivity for the dynamics of biological motion and to the sensitivity to the gravitational forces acting on motion (Simion et al., 2008).

However, because the biological motion display was a structured display (allowing grouping of individual elements), whereas the random motion display was both nonbiological and nonstructured the preference might be explained as a general preference for coherent motion with respect to random, nonstructured stimuli. Moreover, a still open question concerns newborns' sensitivity to some configural or global information revealed by the relative motion of the elements in the biological motion displays. In fact, newborns' preference might be based on both the processing of the dynamic of each single point or of the relationship between the points. For these reasons, the specificity of the biological motion preference, as well as the role of the local and global information in determining the spontaneous preference manifested by humans at birth, was recently investigated in our lab (Bardi et al., in press). In this study, a biological motion stimulus depicting a walking hen was compared with a nonbiological structured motion display representing a hen-like object rotating about its vertical axis (Fig. 6a and b). Newborns exhibited a spontaneous preference toward the biological motion stimulus, revealing that this preference is triggered by the nature of the motion. This result showed that the spontaneous preference for biological motion at birth could be explained on the basis of a specific sensitivity to some dynamic properties of biological motion, which are not shared by the rigid motion of an identical array of dots.

However, on the basis of these results, we could not ascertain if newborns are processing some configural or global information revealed by the relative

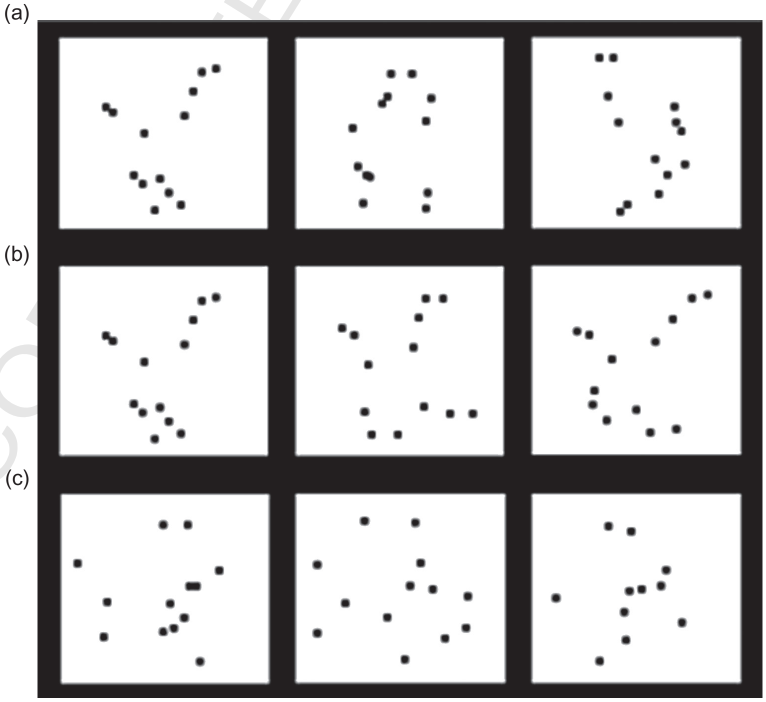

Fig. 6. Three sample frames of the point-light sequences: the rigid motion (a), the walking hen (b), and the scrambled hen (c). (Bardi et al. in press).

motion of the elements in the display, because also the motion of the single dots in the presented stimuli was in fact distinctly different. More precisely in the biological motion sequence, the trajectory of the moving elements was pendular or elliptical, whereas in the rigid motion sequence, all dots underwent a continuous translatory motion as the dots oscillated back and forth along a straight line. Thus, discrimination of the two displays and the obtained preference could be explained on the basis of local motion differences.

To investigate whether newborns are able to process some relations between moving elements in a condition when the movement of the single dot is maintained constant and, thus, whether they are sensitive to some global information of the biological motion stimulus, two experiments were carried out in our lab. In the first experiment, by the use of the habituation technique, newborns' ability to discriminate between a biological display depicting a walking hen and the scrambled version of it was tested. The second experiment tested the spontaneous preference for one of two displays. In the two displays, the movement of each dot was maintained constant but the global disposition of the dot varied. In other words, the scrambled version was created by shifting the starting position of each element and leaving unaltered the local motion (Fig. 6c). Newborns were shown to be able to discriminate the two stimuli revealing that some configural information emerging from the relative motion of the elements in the biological motion stimulus has been processed. However, despite the ability to discriminate between the walking hen and the scrambled version of it, no spontaneous preference between the two displays was present. Therefore, the human system at birth selectively is triggered by the nature of the motion and turns to any biological motion display, irrespective of the animal form it depicts. More intriguing is the fact that, when the dynamic of each single dot is kept constant, no preference emerges. Overall, the information crucial in triggering preference seems to be provided by some invariants contained in the motion of individual dots. However, some degree of configural processing must have been carried out by newborns, because they were able to discriminate between two arrays where the motion of the single dots was equivalent. Therefore, both the biological motion walking hen display and the scrambled version of it have been processed both to the local and global level, similarly to what have been demonstrated to occur for hierarchical geometrical stimuli (Macchi Cassia et al., 2002) and with real faces (Turati et al., 2006).

Overall, the results obtained on newborns support the hypothesis that an inborn predisposition to preferentially process the motion of living creature is present in humans as well as in other animal species (i.e., chicks), before any visual experience.

The empirical evidence collected in our lab supports the notion that adults' expertise in the recognition of the motion of others might originate from an innate predisposition to some properties present in the dynamic of biological motion (Bardi et al., in press; Johnson, 2006; Simion et al., 2008; Troje and Westhoff, 2006). However, preferential attention to biological motion is triggered by the nature of the biological motion irrespective of form aspects, so further evidence needs to be collected to support the idea of the existence of an inborn detection mechanism sensitive to motion of legged vertebrates (Troje and Westhoff, 2006). The newborns' preference for the dynamic of biological motion is supposed to ensure the system to become specialized, later during development, allowing babies to extract fundamental properties of biological motion that convey specific information about conspecifics as form information providing identification of agents.

The role of visual experience in the biological motion perception in the first months of life

While newborns' preference for biological motion at birth is independent of configural properties of the stimulus, it is conceivable that infants' sensitivity to biological motion may encounter a progressive tuning through the visual experience within the species-specific environment. What might in fact develop later through experience is the use of global cues to learn about characteristics of conspecifics, as the nature of the form corresponding to the human body, or to the recognition of social information such as emotion or gender. Evidence showed that by 3–5 months, infants have developed perceptual skills that constrain biological motion perception to organize the displays at the level of the human form. Booth et al. (2002) suggested that the way infants process biological motion could encounter qualitative changes in the early development, as 3-month-old infants appeared to respond primarily to local relations between point-lights in a human biological motion displays, whereas 5-month-old infants appeared to respond primarily to global phase relations when observing biological motion. Infants' developing representation of the human form and its associate gait pattern may contribute to perceptual organization of the biological motion display.

The notion that infants use their developing prototype of human body to extract form from motion is supported by evidence showing that 5-month-old infants cannot discriminate between canonical and perturbed versions of less familiar biological motions, such as those depicting a four-legged spider or a cat (Bertenthal, 1993). Further, the notion that the capacity to organize biological motion displays in a way coherent with the human body form is supported by research findings that demonstrated that at a few months old, infants are able to process properties of human point-light displays necessary for the extraction of a human body form. At 5 months of age, infants can discriminate a point-light walker from one in which the dots' spatial organization and temporal phase are disrupted. Such ability disappeared when the displays were presented upside down (Bertenthal et al., 1987), revealing that infants may use their developing prototype of the human body to constrain the extraction of form from motion. A recent study showed that 6- and 9-month-old infants are able to bind a solid form from human point-light displays. Specifically, infants looked longer to a point-light walker going through a table and violating a solidity principle after habituation with a human point-light stimulus (Moore et al., 2007). Further, there is some evidence that 6- and 9-month-old infants are able to categorize animals and objects on the basis of their pattern of motion (Arterberry and Bornstein, 2001, 2002). Finally, Hirai and Hiraki (2005) showed that the amplitudes of ERPs are higher for intact than for scrambled point-light animations in 8-month-old infants. At this age, ERP amplitudes are also higher for point-light displays that are shown in the upright rather than in the inverted orientation (Reid et al., 2006).

To summarize, biological motion preference at birth seems to depend on the existence of a bias that orient newborns' attention toward certain dynamics properties of the motion. Even if newborns were shown to be sensitive to some configural information revealed by the relative motion of the elements in the biological motion display, such information is not the determinant for the spontaneous preference at birth when the dynamic of the motion is kept constant (Bardi et al., in press). The evidence suggested that infants' sensitivity to biological motion could undergo qualitative changes with the increase of visual experience within the species-specific environment in the first months of life. Such experience may allow the visual system to become specialized in responding to sophisticated properties of conspecifics such a meaning of action, emotion, and intention.

The detailed mechanisms that can extract motion information in the newborn are not yet known. As for face perception, the developmental course of biological motion sensitivity is likely to depend on an interplay between subcortical mechanisms and the development of specific cortical systems. In the future, the development of local and configural processing of biological motion will need to be integrated into the broader knowledge of early subcortical motion processing (e.g., of optic flow and optokinetic control) and the emergence of cortical motion selectivity (Braddick et al., 2003).

Conclusion

The empirical evidence reviewed in this chapter demonstrates the presence of innate predispositions in the human system to detect social stimuli on the basis of some perceptual properties that differentiate them from inanimate objects: the presence of a face and the way they move. These findings are compatible with the Human First Hypothesis (Bonatti et al., 2002), which suggests that humans identify objects and separate conspecifics by using their different properties. The primary role of these innate predispositions is to bootstrap the cognitive system to become fully specialized for social stimuli later during development. The results obtained in our lab on face preference demonstrate that the system is not specialized to process social stimuli from birth and that it is not necessary to hypothesize specific mechanisms for detecting social stimuli. In contrast, general attentional biases are sufficient to explain the preference for face at birth, and the evidence is in favor of a progressive specialization during development as a function of the experience with the social stimuli present in the environment.

Importantly, it has been presented in this chapter that infants' prewired predispositions to face and biological motion encounter qualitative changes with the increase of visual experience within the species-specific environment in the first months of life (Booth et al., 2002; Macchi Cassia et al., 2006; Nelson, 2001; Turati et al., 2005). In other words, these general perceptual constraints become more specific because of interaction with visual experience. These findings highlight the importance of both general constraints of the human visuoperceptual system and exposure to certain experiences shortly after birth, to drive the system to become functionally specialized to process faces and biological motion in the first months of life (Nelson, 2001, 2003).

Finally, preferential attention to faces and biological motion has been interpreted as a precursor to the capacity for attributing intentions to others (Frith and Frith, 1999). This observation raises important issues concerning developmental disorders with core social perceptual deficits, such as autism (Thompson and Hardee, 2008). Autistic Au2 individuals display impairments in the processing of both faces (Hobson et al., 1988) and biological motion (Blake et al., 2003), suggesting a common underlying perceptual basis of these deficits. Recently, it has been shown that 2-year-old children with autism fail to orient toward biological motion, instead manifesting an attentive bias toward nonsocial physical contingencies that are disregarded by children with typical development (Klin et al., 2009). In this vein, future research, providing new insights with regard to how face detection and biological motion perception change across normal and atypical development, may have far-reaching implications for understanding an altered development trajectory of brain specialization.

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