

13 Evolutionary and Neural Bases of the Sense of Animacy

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Evolutionary Bases

In order to detect the presence of a living creature in the environment, an organism can rely on several types of features, or cues, that trigger the automatic detection of *animacy*. These features can be both static and dynamic, resembling basic properties largely shared among different creatures, such as, for instance, the head region or a peculiar way of moving. In this section, we shall summarize and compare the behavioral evidence collected in different animal species about the visual cues that elicit the perception of an animate being.

Static Cues

It happens frequently, we spot illusory funny faces in the accidental placement of objects, clouds, or coffee grounds. This phenomenon is known as “face pareidolia” and has long been believed to be uniquely human (Guthrie & Guthrie, 1993). However, research making use of eye movements has revealed that rhesus monkeys (*Macaca mulatta*) also perceive illusory faces on inanimate objects (Taubert, Wardle, Flessert, Leopold, & Ungerleider, 2017). Faces are indeed a powerful cue to rapidly detect the presence of another creature, and this ability appears early in ontogeny. Human newborns preferentially look at face-like stimuli – three dark blobs triangularly arranged on an oval-shaped background – than at non-face-like configurations of the same stimulus e.g., with the three blobs upside down (Johnson, Dziurawiec, Ellis, & Morton, 1991; Turati, Simion, Milani, & Umiltà, 2002; Farroni et al., 2005; e.g., Figure 13.1). Similarly, infant monkeys (*Macaca fuscata*) do show a non-species-specific preference before any experience with faces (Sugita, 2008). Experience thus seems unnecessary to know that faces are important. This

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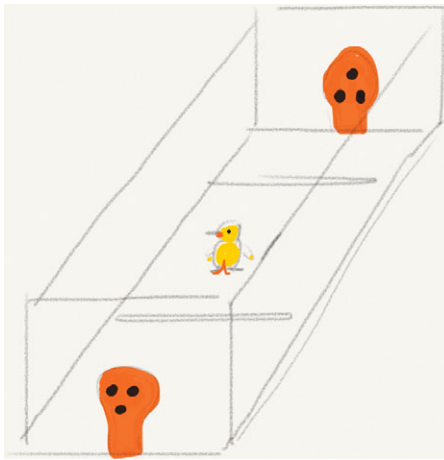


Figure 13.1 Schematic representation of the experimental procedure used to test spontaneous preference for face-like stimuli in chicks (Rosa-Salva, Regolin, & Vallortigara, 2010). Chick is placed in the central sector of a choice runway and is free to approach the two stimuli presented, in this example a face-like and an inverted face-like stimulus.

knowledge could be innate and broadly tuned to focus attention toward salient stimuli for further learning.

The “nature” hypothesis is, however, hard to prove in most mammalian species, and in general, in altricial species, who are difficult to test at birth without any visual experience. From this perspective, precocial species such as domestic chicks (*Gallus gallus*) are a valuable animal model to disentangle the nature/ nurture conundrum (Versace & Vallortigara, 2015; Versace, 2017). Chicks can hatch and be reared in darkness until the test. They are autonomous and with well-developed vision capabilities soon after hatching. Studies with visually naïve chicks show that they prefer a stuffed hen over the same model scrambled in little pieces on a box (Johnson & Horn, 1988). Noteworthy, this preference is also non-species-specific; indeed, chicks do not prefer the hen to a gadwall duck, or even to a polecat. Chicks’ preferential approach is driven by the head–neck configuration present in all these stimuli and not by the single elements composing it (for a review, see Di Giorgio et al., 2017). Subsequent findings confirm the non-species-specificity of this innate face preference, presenting chicks with schematic face-like stimuli and even pictures of human faces (Rosa-Salva, Regolin, & Vallortigara, 2010, 2012; Rosa-Salva, Farroni, Regolin, Vallortigara, & Johnson, 2011; Rosa-Salva, Mayer, & Vallortigara, 2015; see Figure 13.1). Also, there is direct evidence for inherited variability of the hen-like visual preference in naïve chicks (Versace, Fracasso, Baldan, Zotte, & Vallortigara, 2017).

These findings suggest either an early appearance in evolutionary history of this face-detection system shared among distant classes of vertebrates (we

should then observe it also in reptiles), or a mechanism of convergent evolution (for a review, see Leopold & Rhodes, 2010).

Remarkably, such an innate face-detection system is not shared throughout the animal kingdom. Honeybees (*Apis mellifera*) can learn to discriminate and categorize faces from non-faces, using the same configurational strategy used by vertebrates, but they can do it only after specific training (Avarguès-Weber, Portelli, Benard, Dyer, & Giurfa, 2010). On the other hand, a species of paper wasps (*Polistes fuscatus*), characterized by variable facial features used to recognize individual conspecifics, seem to have specialized face-learning abilities (Sheehan & Tibbetts, 2011). A closely related species of wasps (*Polistes metricus*), which does not possess any distinctive facial features, lacks this specialized system, suggesting that different specialized cognitive processes are responsible for different forms of recognition. These findings outline convergent face recognition processes among distant taxa (vertebrates and insects) and divergent species-specific adaptations among closely related species.

Intriguingly, the two horizontal blobs of the schematic face-like stimulus alone are able to elicit in several species of vertebrates a strong antipredator response. Eyes are such powerful cues for vertebrates that some species of invertebrates evolved vertebrate eye-like patterns to dissuade potential predators. For instance, the owl butterfly (*Caligo martia*) owes its name to two conspicuous concentric-circular markings on its wings, mimicking the eyes of an owl. In a study, great tits (*Parus major*), an avid insectivorous species, were presented with Eurasian pygmy owl's eyes, a potential predator (*Glaucidium passerinum*) or with butterfly's eyespots, a potential prey (Bona, Valkonen, López-Sepulcre, & Mappes, 2015). Mimetic eyespots proved to be as effective as true owls' eyes in eliciting aversive responses in tits, demonstrating that eyes alone are a powerful cue to predator animacy.

Apart from a complex role in social interaction based on gaze (for a review, see Emery, 2000), the importance of eyes and eye-like patterns in the perception of predator animacy is observed in various taxonomic groups. A prosimian species, the gray mouse lemur (*Microcebus murinus*), has a selective aversion at looking at pairs of horizontally arranged dots, but not squares (Coss, 1978b). Wild house mice (*Mus musculus*) are faster to escape from a little foot shock when presented with two horizontal yellow light spots (Topál & Csányi, 1994).

Reptiles are also susceptible to eye-like patterns and show a wide variety of reactions to them. Black iguanas (*Ctenosaura similis*), which are prone to human predation, are more likely to escape when the person approaching them is directly (frontally) staring at them and when her eyes are bigger, and thus more salient (Burger, Gochfeld, & Murray, 1991, 1992). Similarly, lizards (*Anolis carolinensis*) exhibit longer tonic immobility, an anti-predatory fear-induced behavior, both when an experimenter is directly looking at them and when dummy eyes with large pupils are shown (Hennig, 1977). Garter snakes

(*Thamnophis sirtalis*) attack realistic eye-pairs (Bern & Herzog, 1994); spitting cobras (*Naja nigricollis*), when threatened, eject their venom precisely in two distinct jets to the eye-region (Westhoff, Tzschätzsch, & Bleckmann, 2005).

As mentioned before, for entire faces, eyes alone are also able to elicit a response at their first presentation to an animal. Hatchling pine snakes (*Pituophis melanoleucus*) exhibit protective flight behavior when exposed to a head model with black eyes and, similar to lizards, neonate hognose snakes (*Heterodon platirhinos*) prolong their tonic immobility, feigning death if a person is directly looking at them (Burghardt & Greene, 1988; Burger, 1998). Interestingly, this is found also in some invertebrates: The blue crab (*Callinectes sapidus*) increases the duration of tonic immobility when presented with artificial eyes staring directly at it (O'Brien & Dunlap, 1975).

Chickens, as is the case for many species of birds, perceive the direct gaze of a person or of a couple of artificial eyes as a threat (Gallup, Cummings, & Nash, 1972; Jones, 1980; Vallortigara & Zanforlin, 1988; Rosa-Salva, Regolin, & Vallortigara, 2007). These findings, together with the spontaneous preference for faces, may appear contradictory. In fact, eye-avoidance is also hypothesized to be unlearned (Scaife, 1976a, 1976b; Emery, 2000). It could be that the addition of a third spot in the face-like configuration makes the transition from a frightening (eyespot) to an attractive (face-like) stimulus (and that the second signal evolved in some way from the first). Also, the difference may arise at a different developmental time-point for the two predispositions. In chicks, face-preference studies found a spontaneous non-species-specific preference for faces in newly hatched, visually naïve chicks prior to visual imprinting (Rosa-Salva et al., 2015). In contrast, eye-avoidance studies typically test chicks that are at least one-week old, after filial imprinting has occurred (Gallup et al., 1972; Jones, 1980; Rosa-Salva et al., 2007). Possibly, soon after hatching, chicks need to imprint on the most animate object available and here the face preference facilitates this process. After imprinting has occurred, chicks have to maximize their survival by following the learned conspecific and avoiding all other eye-predators.

This hypothesis is strengthened by studies on jewel fish (*Hemichromis bimaculatus*), which possesses an innate mechanism to discriminate the two-facing eyes of other fishes (Coss, 1979). At an early stage of development, fry do not preferentially approach or avoid face-like stimuli. Then, after thirty days they consistently avoid all stimuli presenting two-facing eyes, e.g., they avoid swimming in the portion of space frontal to their parents (Coss, 1978a). Interestingly, tortoises (*Testudo* sp.), a precocial species with no parental care, seem to have an early mechanism discriminating face-like stimuli, possibly facilitating dispersal soon after hatching (Versace, Damini, Caffini, & Stancher, 2018).

Similar to the widespread aversion to eyes to avoid predation, primates probably evolved a rapid mechanism to spot threatening animate stimuli, such as snakes (Isbell, 2009; Headland & Greene, 2011). It is estimated that humans

suffer between 1.2 to 5.5 million snakebites per year worldwide (Kasturiratne et al., 2008). Such a staggering rate may explain the biological importance of evolving a predisposed template for detecting snakes quickly. Snakes, as well as spiders, are detected faster than innocuous stimuli by human adults, pre-school children and macaque monkeys (*Macaca fuscata*; Öhman, Flykt, & Esteves, 2001; Shibasaki & Kawai, 2009; LoBue & DeLoache, 2010). Moreover, differential skin conductance, a measure of arousal, reveals that human responses to fear-relevant stimuli such as spiders and snakes are already activated prior to consciously perceiving them (Öhman & Soares, 1993).

As described for the eyespots on moths' wings, which perfectly imitate owl's eyes, a similar phenomenon is observable in the larvae of hawk moths (*Sphingidae* sp.), which closely resemble a viper's head (Bates, 1862). When threatened, these larvae hide their heads, inflate the abdomen in a flat triangular fashion on which two symmetrical, large black spots are clearly visible, and throw themselves backward hanging from the branch. This sequence of behaviors creates a perfect imitation of a small tree viper (a venomous snake). Henry Walter Bates (1825–1892), the father of scientific mimicry studies, wrote about this, which he described as the most extraordinary example of imitation he encountered: “*I carried off the Caterpillar, and alarmed every one in the village*” (Bates, 1862). The mimic octopus, an Indo-Malayan species (*Thaumoctopus mimicus*), chooses its frightening camouflages appropriately in different situations, ranging from different threatening sea animals such as the venomous lion-fish (*Pterois* sp.), but is also exceptionally good in feigning the banded sea-snake (*Laticauda* sp.; Norman, Finn, & Tregenza, 2001).

Another typical feature of terrestrial mammals is fur. Almost every child has a furry puppet to hug, play and even sleep with. Interestingly, three-month-old macaque monkeys (*Macaca fuscata*) prefer to look longer at a fluffy stone than a stone without fur (Tsutsumi, Ushitani, Tomonaga, & Fujita, 2012), suggesting that fur could be an efficient cue to elicit *animacy* perception. Traditional experiments on social deprivation of infant monkeys (*Macaca mulatta*) revealed that monkeys isolated from their mother and conspecifics were less affected by this social deprivation when provided with a so-called mother surrogate made of cloth (Harlow & Suomi, 1971). Surprisingly, when provided with a choice between a wire-covered mother surrogate feeding them with milk and a cloth-covered surrogate without milk, young monkeys consistently preferred to interact with the comfortable (but not feeding) surrogate mother (Harlow, 1958; Suomi & Leroy, 1982). Further evidence is required to shed some light on the fluffy-soft cue to *animacy* and its evolutionary origins.

Young human infants possess some sort of expectation about the fact that animals have innards (Setoh, Wu, Baillargeon, & Gelman, 2013). Indeed, when an animate object is hollow, infants look longer at it, demonstrating surprise about this fact. On the contrary, visually naïve newly hatched chicks

show a spontaneous preference for hollow objects (Versace, Schill, Nencini, & Vallortigara, 2016). This evidence combined suggests that experience may be important, at least in humans, to learn that animate beings have innards.

Dynamic Cues

Faced with an awkward social situation, one may feel the need to disappear unnoticed by executing the crab-walk: moving sideways in a furtive manner. Many crab species, indeed, walk sideways, which is uncommon in the animal kingdom. It is uncommon because *bilateria*, animals with a symmetrical arrangement around one of their main body planes (Hatschek, 1888), usually move along their main body axis. While moving in the direction of their eyes, they maintain a consistent antero-posterior orientation. This could be a defining feature to predict the direction of animal motion. Instead, violations to this general attitude, such as the crab-walk, could improve survival for prey species, increasing the unpredictability of their escape trajectory from predators.

Based on this widely shared motion habit, tentacled snakes (*Erpeton tentaculatus*) are able to predict the direction of future movement of their fish prey (Catania, 2009). Many teleost fishes have a fast and efficient escape mechanism with respect to stimuli approaching suddenly, called the C-start reaction (Eaton, Bombardieri, & Meyer, 1977). When they perceive a water disturbance on one side of their body, they bend into a C-shape and suddenly swim in the other direction. Tentacled snakes have adapted to triggering the fish escape response, by feigning an approach on one side with their body, and striking on the other side (to which fish usually escape) with their jaws wide open. They are also able to predict where the fish will move, even before it actually starts to move, using the fish's antero-posterior orientation with respect to its head (Catania, 2009). This suggests that snakes are sensitive to head direction, and are able to use this cue to predict an animate movement accordingly.

Starting from six months of age, human infants rely on the axis alignment of movement with respect to the facial features to predict trajectories of artificial objects (Hernik, Fearon, & Csibra, 2014). Indeed, to induce expectations on the trajectory, it is enough to make distinguishable the two extremities of an elongated moving object (see Figure 13.2). For instance, a mark on one of the two extremities will recreate an antero-posterior organization of the moving object and consequently make trajectories predictable (Hernik et al., 2014).

The direction of motion with respect to the main body axis and its consistency in time, even without any facial feature, is a strong cue for *animacy per se*. This cue can help animals to distinguish the movement of an animate being from an inanimate one, and the movement of a prey from the movement of a predator. Toads (*Anura* sp.), which rely on motion to detect prey, do not see



Figure 13.2 Examples of simple moving stimuli used for studying axis alignment. In the first example, an asymmetry on one side of a bar together with movement is enough to interpret it as a head and predict future direction of motion. In the second example, movement along (worm) and orthogonal (anti-worm) to the main body axis. Similar stimuli are found to trigger respectively prey-catching and anti-predatory responses in toads (Ewert, 1987).

stationary objects, due to the absence of saccadic eye movements, and use the direction of movement with respect to its main axis to catch prey (Ewert, 1987, 2004). In laboratory conditions, toads will snap at a bar moving along its longer body axis (worm configuration), interpreting it as prey, and will avoid the same object moving orthogonally to its longer body axis (anti-worm), interpreting it as a threat (see Figure 13.2; Ewert, 1987).

When adding a mark on one end of the worm configuration of motion, toads will preferentially strike at that position of the bar, demonstrating interpreting it as a head. Indeed, for toads it is biologically advantageous to snap at prey in the head region to maximize the probability of catching them; snaps at the “tail” region will most frequently result in striking behind the moving prey (Ewert, 2004). Similarly, the mudskipper, an amphibious fish feeding on earthworms, displays the same behavior (Kutschera, Burghagen, & Ewert, 2008). This similarity in prey-catching behavior in toads and amphibious fishes has been hypothesized to be the product of convergent evolution in a similar habitat with similar selection pressures (Kutschera et al., 2008).

Another terrestrial vertebrate, the chick, is able to discriminate between objects moving orthogonally and along their longer body axis (Clara, Regolin, Vallortigara, & Rogers, 2009). One-day old chicks show a spontaneous preference for pecking at elongated insect-like stimuli never experienced before, but only when they move orthogonally in relation to their longer body axis. Contrary to what is observed in tetrapods and amphibian fishes, however, this response may enhance the probability of young chicks catching prey that are already wounded (Clara et al., 2009).

Moving from prey *animacy* to social attraction, visually naïve chicks spontaneously approach simple objects that move along their longer body axis (Rosa-Salva, Hernik, Broseghini, & Vallortigara, 2018). Contrary to their feeding preference, chicks exhibit social preference for the same type of motion that human infants evaluate as animate (Hernik et al., 2014). All this evidence together highlights how animate motion is usually characterized by the

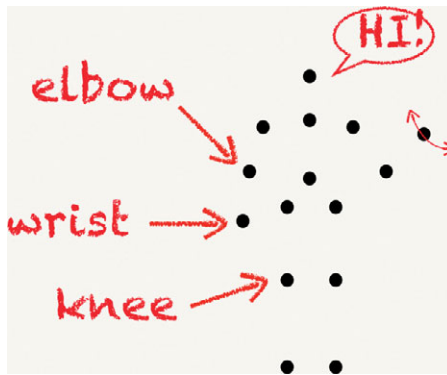


Figure 13.3 Schematic representation of a point-light display with a person standing and shaking his left hand.

physical constraints of animals, and that the detection of animate motion cues emerges early in ontogeny and is widely shared among different animals.

The motion of an animal in general is more attractive to other animals than the motion of a windblown tree, for instance. Lizards (*Anolis sagrei*) presented with videotapes of real wild animals in their visual periphery, in such a way to prevent high-resolution vision, are faster to direct their attention toward animal movements than to vegetation movements caused by the wind (Pallus, Fleishman, & Castonguay, 2010). To prevent static visual features from interfering with the analysis of biological motion, animations have been created using dark spots on a white background placed on the joints of an invisible animal walking (point-light display; e.g., Figure 13.3).

Visually naïve chicks demonstrate a non-species-specific spontaneous preference to approach these biological motion stimuli resembling a walking hen or even a cat over the same dots rigidly rotating or moving randomly (Vallortigara, Regolin, & Marconato, 2005; Vallortigara & Regolin, 2006). A similar looking preference is shown by human neonates using almost identical stimuli (Simion, Regolin, & Bulf, 2008), by dogs (*Canis familiaris*; Kovács et al., 2016) and by marmosets (*Callithrix jacchus*; Brown, Kaplan, Rogers, & Vallortigara, 2010).

The ability to discriminate biological motion displayed by point-light displays is shared by distant classes of vertebrates. Different species of teleost fishes (*Pseudotropheus zebra*, *Dascyllus aruanus*, *Oryzias latipes*) perceive and distinguish biological motion patterns depicted in point-light displays (Nakayasu & Watanabe, 2013; Schluessel, Kortekamp, Cortes, Klein, & Bleckmann, 2015). Studies investigating shoaling behavior, i.e., the tendency to swim together with a group of conspecifics, found that both the posture and the trajectory of motion displayed by the shoal can drive fishes' attraction to biological motion (Larsch & Baier, 2018; Shibai et al., 2018).

It has been postulated that the main feature driving the perception of biological motion is the peculiar semi-rigidity typical of legged animals (Vallortigara et al., 2005). Two dots from the point-light display, i.e., the elbow point and the wrist point, will always maintain their distance fixed with respect to each other, unless you broke your arm, while changing the relative distances with the other dots, i.e., the knee point (see Figure 13.3).

Trying to understand the more elementary motion features that characterize the motion of living organisms, a more basic feature that makes all animate beings different from inanimate objects is the presence of an internal energy source, as postulated already by Aristotle (Aristotle, 1980). If the cup of coffee on your desk should now start to move on its own, you would immediately stop reading and pay attention to this weird and unlikely phenomenon. We all know that inanimate objects do not move on their own, only if something else acts on them. So, if an object moves on its own, it is highly probable that it is alive.

Newly hatched chicks demonstrate a preference for self-propelled objects. After being imprinted on a simple video animation, in which object A starts to move on its own, stops near stationary object B, which immediately starts to move after being pushed by A, chicks prefer to approach A (Mascalzoni, Regolin, & Vallortigara, 2010). This preferential “imprintability” reveals that chicks spontaneously discriminate between animate and inanimate movements by using start-from-rest as a cue for self-propulsion. In fact, the presence of an internal energy source can be inferred from self-propulsion, the ability to autonomously change the state of motion (Premack, 1990). Cues of self-propulsion include: start-from-rest, changes in speed, changes in trajectory, and movements against gravity. In a similar vein, human neonates preferentially look at simple objects starting from rest (Di Giorgio, Lunghi, Simion, & Vallortigara, 2016), as well as three-month old Japanese macaques (*Macaca fuscata*), which preferentially look at a self-propelled stone (Tsutsumi et al., 2012).

Surprisingly, even more subtle changes in the state of motion, such as speed changes without start-from-rest, are able alone to elicit a strong spontaneous preference few hours after hatching in visually naïve chicks (Rosa-Salva, Grassi, Lorenzi, Regolin, & Vallortigara, 2016). In a spontaneous-preference task, chicks are free to choose between a simple object accelerating and decelerating and an identical one moving at constant speed. In a crucial control condition, the two single moments of speed change are occluded and, remarkably, the chicks’ preference disappears, thus demonstrating that visible speed changes are cueing the perception of *animacy* (Rosa-Salva et al., 2016).

As discussed for the role of eyes in the first section, looming provides a strong dynamic cue for predatory attack. A variety of animal species e.g., fish, amphibians, crustaceans, insects, birds, monkeys, mice, human infants, and chicks exhibit diverse fear behaviors in response to a shadow progressively

increasing in size, as something rapidly approaching from above (Schiff, Caviness, & Gibson, 1962; Ball & Tronick, 1971; King Jr., Lettvin, & Gruberg, 1999; Barrett, 2005; Preuss, Osei-Bonsu, Weiss, Wang, & Faber, 2006; Oliva, Medan, & Tomsic, 2007; Fotowat, Harrison, & Gabbiani, 2011; Yilmaz & Meister, 2013; Hébert, Versace & Vallortigara, 2019). Looming stimuli, like other stimuli presented from above, commonly elicit fear and are perceived as a threat, whatever they are. Upon spotting something flying above you (predator) or something falling on you (stone), it is better to flee. Mice (*Mus musculus*), as well as newly hatched chicks, show selective innate responses to two different shadows moving from above (De Franceschi, Vivattanasarn, Saleem, & Solomon, 2016; Hébert, Versace & Vallortigara, 2019). When a black disk is rapidly increasing in size (looming), they spontaneously run away and try to hide beneath something. In contrast, when a small disk sweeps from above, without increasing in size, they tend to freeze and stay motionless. These differential responses suggest the existence of a selective mechanism that has evolved to respond appropriately to different simple stimuli moving overhead. If something is rapidly approaching you, the best choice for survival is to escape from it, as probably the predator has already seen you; if something is flying above in the distance it is better to freeze, maximizing the possibility of remaining unnoticed (De Franceschi et al., 2016).

The evidence reviewed here strongly supports the idea of a set of unlearned rudimentary knowledge mechanisms about animate beings hardwired to tune vertebrates' cognitive systems toward the most salient object surrounding them, the next section will briefly summarize the neural evidence collected so far supporting this innate knowledge and the related behavioral responses.

Neural Bases

The neural mechanisms underlying the rapid detection of animals could be partially homologous in different classes of vertebrates, and elicit *fast and dirty* responses redirecting attention toward potentially salient stimuli for further learning, as in the case of neonate animals, or for further classification of the object and proper behavioral responses for adult animals. Contrary to the relatively abundant literature about the behavioral level of analysis, the neuronal substrates underlying unlearned knowledge about *animacy* have been less investigated.

Static Cues

Studies on chicks' filial imprinting (Vallortigara & Versace, 2018) inspired a two-process theory about the different neural mechanisms that underlie

unlearned preferences for the choice of the imprinting object and subsequent learning of this imprinting object (Johnson, Bolhuis, & Horn, 1985).

It has been hypothesized that a subpallial component would bias unexperienced chicks' attention toward the most appropriate object in the environment and serve as a guide for a pallial component that mediates learning through massive exposure of the more specific and individual features of the object selectively attended to (Johnson et al., 1985). These two processes would be subtended by highly independent brain structures (Horn & McCabe, 1984; Johnson & Horn, 1987). The first predisposed mechanism has been hypothesized to involve the optic tectum, the avian homologue of the mammalian superior colliculus, part of the subcortical collothalamoc visual pathway (Butler & Hodos, 2005; Wylie, Gutierrez-Ibanez, Pakan, & Iwaniuk, 2009; Johnson, Senju, & Tomalski, 2015). Indeed, there is indirect evidence for a dissociation between the neural correlates of predisposed and learned preference (Horn & McCabe, 1984; Johnson & Horn, 1987). A restricted region of the chick forebrain is involved in learning the features of the imprinting object, the intermediate medial mesopallium (IMM; for a review, see Horn, 2004). Lesion to this region impairs acquisition and retention of the imprinting memory, but interestingly the impairment is more pronounced when imprinting has occurred, before the lesion, on an artificial object rather than on a predisposed one (e.g., a naturalistic stimulus like a stuffed jungle fowl; Horn & McCabe, 1984; Johnson & Horn, 1987). Similarly, immediate early gene (IEG) expression, commonly used as a neural plasticity marker, reveals a greater plasticity in the IMM of chicks that approached a scrambled version of the jungle fowl (cut in little pieces and reassembled on a box, clearly an artificial object) compared to the IMM of chicks that approached an intact fowl (Mayer, Rosa-Salva, Lorenzi, & Vallortigara, 2016), confirming the different involvement of this area when non-predisposed stimuli have to be learned.

The IMM is a telencephalic associative region, which has been hypothesized to be involved in learning to discriminate between individual conspecifics (Johnson & Horn, 1986). Bilateral lesions to IMM impair recognition of the particular jungle fowl to which chicks have been previously exposed, while lesion to the visual Wulst (thought to be a homologue of the visual cortex in mammals, V1; Butler & Hodos, 2005) does not impair the individual recognition (Johnson & Horn, 1986).

Inspired by this evidence, a two-process theory for face-processing is formulated for human neonates (Morton & Johnson, 1991; Johnson et al., 2015). One process, devoted to the early detection of a broad category of face-like stimuli and active from birth, is called CONSPEC. A second process, called CONLERN, developing and specializing through exposure, is devoted to the discrimination and recognition of individual faces (Johnson et al., 2015).

Similarly in humans, CONLERN, comprising cortical areas, specializes in faces after receiving selective exposure provided by CONSPEC (Johnson

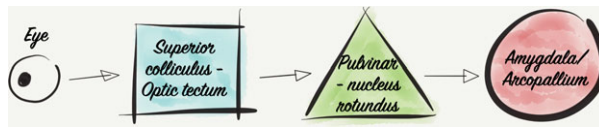


Figure 13.4 Schematic representation of the subcortical visual pathway supposed to be involved in directing attention toward biologically relevant stimuli in different vertebrates (Sewards & Sewards, 2002; Johnson, 2005). Direct afferences from the eye project to the superior colliculus (for mammals, optic tectum for other vertebrates), from which it goes to the pulvinar in the thalamus (nucleus rotundus in other vertebrates) and finally reaches the amygdala (arcopallium believed to be partially homologue in birds; Martínez-García, Novejarque, & Lanuza, 2008; Ikebuchi et al., 2012).

et al., 2015). Supporting this hypothesis, in adults an extrastriate region specializes in face perception and individual recognition, the fusiform face area (Kanwisher, McDermott, & Chun, 1997; Haxby, Hoffman, & Gobbini, 2000). Noteworthy, face pareidolia in adults and face-like patterns in neonates involve this same region (Liu et al., 2014; Buiatti et al., 2019), suggesting an early involvement of the cortical route in the processing of face-like stimuli.

Moving to the neural substrates underlying the predisposed mechanism for detecting faces, CONSPEC, several authors have hypothesized an involvement of the subcortical visual pathway that would include the superior colliculus, the pulvinar and the amygdala (see Figure 13.4; Johnson, 2005). More recent evidence suggests an extended involvement of this subcortical route in orienting attention toward a broader category of stimuli relevant for survival since birth (Sewards & Sewards, 2002; Öhman, 2005; Adolphs, 2008; Day-Brown, Wei, Chomsung, Petry, & Bickford, 2010; Tamietto & de Gelder, 2010; Maior et al., 2012; Nakano, Higashida, & Kitazawa, 2013; Nguyen et al., 2013, 2014). From this perspective, we will now summarize neural evidence for each neural component of the subcortical route.

Electrophysiological recordings from single neurons in the amygdala of rhesus monkeys reveal selective responses for faces, with small or no response to arousing and aversive stimuli such as looming objects (Leonard, Rolls, Wilson, & Baylis, 1985). High resolution fMRI shows an involvement of rhesus monkeys' amygdala during presentation of threatening face expressions and of faces with averted gaze (Hoffman, Gothard, Schmid, & Logothetis, 2007). Similar activity is observed in adult humans in the amygdala for masked, at low spatial frequency, facial stimuli as well as masked images of threatening animals (e.g., snakes), suggesting that the amygdala's activation could be mediated by the superior colliculus and pulvinar (Öhman, 2005).

In domestic chicks, first exposure to a live conspecific involves the arcopallium (Mayer, Rosa-Salva, Morbioli, & Vallortigara, 2017; Mayer, Rosa-Salva, & Vallortigara, 2017), which is believed to be partially homologue to the mammalian amygdala (Martínez-García et al., 2008; Ikebuchi,

Nanbu, Okanoya, Suzuki, & Bischof, 2012). Involvement of the arcopallium seems to be selective for static features present in the live conspecific. Indeed, when chicks exposed to a live conspecific are compared with chicks presented with a stuffed rotating chick, the arcopallium seems to be equally involved in both groups (auditory stimulation balanced; Mayer et al., 2017; Mayer, Rosa-Salva, & Vallortigara, 2017). In line with this hypothesis, an fMRI study on human adults finds no differences in the amygdala when different dynamic facial expressions are presented (van der Gaag, Minderaa, & Keysers, 2007), while other studies find differences in the amygdala when presented with static pictures of different facial expressions (Phan, Wager, Taylor, & Liberzon, 2002).

The superior colliculus and pulvinar are midbrain regions highly conserved among vertebrates (respectively, the optic tectum and the nucleus rotundus in the avian brain; Ebbesson, 1972; Butler & Hodos, 2005), which are involved in saccadic/head-orienting movements (Masino & Knudsen, 1992; Schmidt & Bischof, 2001; Trappenberg, Dorris, Munoz, & Klein, 2001). The superior colliculus is a layered structure and its outer layers receive direct visual inputs from the retina (Leventhal, Rodieck, & Dreher, 1981; Perry & Cowey, 1984; Rodieck & Watanabe, 1993). In rhesus monkeys, single neurons in the superficial layers are selective for a wide variety of faces and face-like stimuli (Nguyen et al., 2014). Soon after stimulus onset, some neurons preferentially encode all facial stimuli and filter them for rapid processing of raw facial information. During later phases, the categorization of the stimulus is detectable from the clustering of neurons responding to different characteristic of the stimuli, i.e., a cluster for frontal and one for profile pictures (Nguyen et al., 2014).

Bilateral lesions of the superior colliculus in infant capuchin monkeys (*Cebus*) produce only a transitory impairment in spontaneous social behavior but a stable deficit in the recognition of threats (Maior et al., 2011). Lesioned subjects do not avoid taking a piece of banana when a rubber snake is nearby, while sham-operated monkeys avoid the dangerous banana-snack (Maior et al., 2011).

Potentially, the superior colliculus in infancy could subtend both spontaneous social mechanisms and detection of threats; after maturation of cortical areas the social function of the superior colliculus may be hidden or compensated from the activity of cortical structures, while maintaining the threat detection function (Maior et al., 2012). In adulthood, the superior colliculus may therefore represent a rapid mediator for fast behavioral responses to salient stimuli bypassing cortical control (Day-Brown et al., 2010). In rodents, electrical stimulation of two different regions of the deeper layers of the superior colliculus initiates two different behavioral responses, orienting for approach and flight for avoidance (Sahibzada, Dean, & Redgrave, 1986; Dean, Redgrave, & Westby, 1989).

The pulvinar, a thalamic nucleus, plays an important role in directing attention and sending relevant information to the visual cortex (Saalmann,

Pinsk, Wang, Li, & Kastner, 2012). As described regarding the superior colliculus, electrophysiological recordings in monkeys (*Macaca fuscata*) reveal the presence of neurons sensitive to a broad variety of face-like stimuli, rapidly activated after stimulus onset and later differentiated by the clustering of neuronal responses into categories of visual properties (Nguyen et al., 2013). Interestingly, other neurons in the pulvinar respond selectively to snake images and not to faces (Van Le et al., 2013).

This evidence extends the role of the subcortical visual pathway initially hypothesized to be relevant for social predispositions (Johnson et al., 1985; Morton & Johnson, 1991) to a broader category of animate stimuli relevant for survival, namely social companions and predators. Moreover, it suggests an inborn brain organization that differentiates into relevant categories of animate stimuli in the early stages of visual processing, even before any learning has occurred. It is important to highlight that early involvement of the specialized cortical network for schematic faces has been observed already in human neonates, suggesting also a cortical involvement prior to experience-dependent learning (Buiatti et al., 2019).

Dynamic Cues

Pioneering studies with anurans have investigated the role of the optic tectum (Ingle, 1973; Kostyk & Grobstein, 1982; Ewert, 1987) in detecting prey and predators. Prey-selective neurons have been found in this region (Weerasuriya & Ewert, 1981) and lesion studies reveal a complete loss of responsiveness to prey and predators (Ingle, 1973; Kostyk & Grobstein, 1982). The same stimuli used for prey–predator studies in anurans have been used to record single-cell activity in mice’s superior colliculus (Manteuffel & Fiseifis, 1990). The neuronal responses recorded are very similar to those in the anuran optic tectum, showing selectivity for different static and dynamic features. Thus, the tectal responsiveness to configurations is hypothesized to be a plesiomorphic tetrapod character (i.e., an ancestral character shared among vertebrate taxa) resulting from basic structural properties of the tectum (Manteuffel & Fiseifis, 1990). In birds, some neurons of the optic tectum respond selectively to simple characteristics of motion, such as its direction, but no evidence for selective responses to animate motion has yet been observed (Frost & Nakayama, 1983; Frost, Cavanagh, & Morgan, 1988; Luksch, Cox, & Karten, 1998; Verhaal & Luksch, 2016).

Using point-light displays depicting biological motion, fMRI studies in humans and single-unit recordings in monkeys have found a specialized neural network, comprising in its core the right posterior superior temporal sulcus, which is different from that processing other types of moving stimuli (for a comprehensive review, see Pavlova, 2012). Apart from such cortical involvement in biological motion processing, there is evidence for a bidirectional loop between the right posterior superior temporal sulcus and the left cerebellum in

humans (Sokolov et al., 2012), pointing to a possible involvement of the cerebellum in social cognitive functions and in the discrimination of biological motion.

More naturalistic studies, investigating the first exposure to a moving conspecific in visually naïve newly hatched chicks have found an involvement of septum and preoptic area of the hypothalamus (Mayer, Rosa-Salva, & Vallortigara, 2017; Mayer et al., 2017). These two brain regions are nodes of the so-called Social Behavior Network (Newman, 1999), composed of areas well interconnected to each other, rich in sex-steroid hormone receptors, and known to be involved in many complex adult social behaviors and highly conserved in birds and mammals (O'Connell & Hofmann, 2011; homologies have been proposed for all vertebrates, but see Goodson & Kingsbury, 2013). Differences in IEG expression are found in the septum and preoptic area between chicks exposed for the first time to a live chick or to a stuffed rotating one (Mayer et al., 2017). The only differences between the two groups rely on the type of motion and on the contingency between beak movements and the sounds produced (static visual features and auditory stimulation are identical for both groups). This evidence suggests that the septum and preoptic area are potentially involved in early processing and/or approaching animate objects. To further investigate this hypothesis, a more controlled elementary motion cue to self-propulsion has been used in visually naïve newly hatched chicks (developed in Rosa-Salva et al., 2016). Two groups of chicks are briefly exposed to either a speed-changing stimulus, which is a cue of self-propulsion, or a constant moving one (Lorenzi, Mayer, Rosa-Salva, & Vallortigara, 2017). The septum and preoptic area show higher expression of IEG in the group exposed to self-propulsion. These results point to a precocial involvement of the Social Behavior Network in processing early predisposed motion stimuli. Interestingly, these predispositions and the associated brain correlates, are affected by substances modulating social responses, such as mesotocin, the avian equivalent for oxytocin (Loveland, Stewart & Vallortigara, 2019), and valproic acid (Sgadò, Rosa-Salva, Versace, & Vallortigara, 2018; Lorenzi et al., 2019).

With regard to the most elementary motion cues that trigger antipredator and fear responses among distant clades, the neural correlates of looming stimuli have been extensively studied. Neurons in the superior colliculus of mice strongly respond and speed-tune to approaching looming stimuli (Zhao, Liu, & Cang, 2014). Moreover, parvalbumin-positive excitatory projection neurons in the superior colliculus of mice play a key role in detecting approaching stimuli (Shang et al., 2015). Intriguingly, two distinct groups of these neurons underlie two separate tectofugal pathways giving raise to two divergent behavioral responses, escape and freezing (Shang et al., 2018). Remarkably, at the behavioral level these defensive behaviors are triggered by two different overhead stimuli (looming/escape, sweeping/freeze; De Franceschi et al., 2016), it is thus reasonable to hypothesize that these

two subpopulations could be responsible for the difference observed at the behavioral level.

In the pigeon's (*Columba livia*) nucleus rotundus thalami, the second hub after the optic tectum in the subcortical visual pathway, exist three subpopulations of neurons selective to looming stimuli (Sun & Frost, 1998). Each of these subpopulations responds to a different optical variable related to image expansion of the moving stimulus. These variables, taken together, provide a precise “time-to-collision” estimation and an early warning to escape (Sun & Frost, 1998).

Intracellular recordings in the crab (*Chasmagnathus granulatus*) reveal the presence of neurons in the lobula (third optic neuropil) responding to a looming stimulus. The activity of these neurons positively correlates with the behavioral escape response (Oliva et al., 2007). After stimulus onset, the spike frequency progressively increases as the stimulus approaches the subject, this firing rate somehow simulating the expansion rate of the retinal image of the stimulus (Oliva et al., 2007). Similarly, locusts (*Schistocerca americana*) and fruit flies (*Drosophila melanogaster*) have some neurons highly sensitive to looming stimuli in the lobula giant movement detector, with direct projections to motor neurons for rapid escape behavior (Fotowat & Gabbiani, 2007; Fotowat et al., 2011; Dewell & Gabbiani, 2012).

Conclusion

It is apparent from the evidence summarized here that the selective pressures to rapidly detect and respond to the presence of other living beings have shaped, through evolution, the brain and behavior of distant animal species in similar ways. It is highly advantageous for animals to be equipped from birth with preprogrammed mechanisms for orienting their attention toward salient categories of stimuli, instead of having to learn them through long sequences of trial and error. This also lays the foundations for further developmental refinement. Learning mechanisms will capitalize on such innate equipment that channels attention toward salient categories of stimuli and events, refining the behavioral and cognitive repertoire.

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