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Review

Threat-detection in child development: An evolutionary perspective

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ABSTRACT

Evidence for developmental aspects of fear-targets and anxiety suggests a complex but stable pattern whereby specific kinds of fears emerge at different periods of development. This developmental schedule seems appropriate to dangers encountered repeatedly during human evolution. Also consistent with evolutionary perspective, the threat-detection systems are domain-specific, comprising different kinds of cues to do with predation, intraspecific violence, contamination–contagion and status loss. Proper evolutionary models may also be relevant to outstanding issues in the domain, notably the connections between typical development and pathology.

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Children’s fears would seem a prime example of irrational and dysfunctional cognition, as they in most cases target non-existent dangers or unlikely outcomes. In this review, we show how the evidence contradicts this picture, and suggests a highly functional system, finely calibrated to the child’s specific circumstances. Beyond this, developmental data illuminate important issues such as the connection between fear and anxiety, the role of the imagination in human threat-detection, and the role of our evolutionary history in shaping human responses to potential danger.

A biological and psychological approach to human threat-detection and precautionary psychology should pay special attention to the developmental processes involved, for several reasons. First, children grow in very different environments and must develop efficient strategies against very different kinds of dangers. Commonalities and differences in precautionary psychology

across cultures can tell us a lot about the underlying processes (see Lienard, *this issue*). Second, human children go through a long maturation period, with major changes in potential dangers and reactions. From an evolutionary perspective, we would expect children to develop age-appropriate threat-detection and responses. This in turn should connect to and enrich what we know of the development of emotional and cognitive systems in childhood. Third, some pathologies of threat-detection, such as obsessive–compulsive disorder (OCD) or social anxiety, often emerge during childhood and early adolescence, to some extent as a harmful exaggeration of typical responses, which is why it may be of great help to have an integrated picture of typical development in this domain.

In what follows we summarize an empirical literature that spans the whole of child development as well as a variety of domains of potential threat and precautionary responses. It would be misleading to call this a “state of the art”, however, as the domain of research is not properly integrated, or not yet. That is, relevant findings and models are scattered in the child development literature, but also in clinical studies, anthropological comparisons,

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and evolutionary modeling. There is no unified field of research on threat-detection in children, with remarkable exceptions (Evans et al., 1997). The aim of the present survey is to suggest that this is indeed a proper domain of inquiry, despite disciplinary boundaries.

1. Developmental schedule of fear-targets

A number of authors have noted that different domains of fear come online during human development. Stanley Hall's survey was perhaps the first systematic attempt to measure the prevalence of common fears on a large sample of children and adolescents, documenting the salience of natural triggers (thunder, reptiles, insects) as well as situational (darkness) and social ones (Hall, 1897).

Very broadly, one can delineate a general developmental schedule for typical childhood fears, starting with specific situations in infancy, moving on to specific targets like monsters and animals in early childhood, while fears of accidents, injury or contagion appear slightly later (middle to late childhood), and social threats appear in late childhood and become salient in early adolescence (for surveys, see (Field et al., 2001; Muris et al., 1997).

As infants cannot initiate movement or precautionary action, their only defense is active protection from caregivers, which suggests that the most dangerous situation is simply the physical absence of caregivers, or the presence of adults other than caregivers (Scarr and Salapatek, 1970), see also Hahn-Holbrook (this issue). Stranger anxiety develops early in infants (around 8 months) and persists until the toddler years. A variety of behaviors signal the infant's distress when approached by non-familiar people, especially adults and especially males. Stranger anxiety is not dependent on the kind of experience the child has had with strangers – so that children used to daycare as opposed to nuclear family environments do not evince substantially different reactions. Reactions to strangers are partly modulated by social referencing (using the caregiver's reaction as a cue to behavior) (de Rosnay et al., 2006) which is also why socially anxious mothers communicate their anxiety to infants (Murray et al., 2008).

The beginnings of early childhood (from 18 months to 5 years) coincide with the emergence of active exploration of the environment and potential encounters with dangers that children have neither the physical strength nor the cognitive equipment to deal with. Early exploration still includes typical fears of infancy, notably stranger anxiety that is modeled from the mother (Egliston and Rapee, 2007). Attachment styles also play a role in the development of safety feelings in the exploration of new environments (Dallaire and Weinraub, 2007; Grossmann et al., 2008).

The typical fears of early and middle childhood target monsters and other kinds of mysterious intruders. Most children spontaneously provide minimal descriptions of these entities, often enriched with material from folktales or cartoons (Sharon and Woolley, 2004). An unpublished survey of childhood fears and rituals run in our lab confirmed, on the basis of parents' reports, that monsters/animals are a prime concern at that age. Direct testing of the children, when asked to suggest what stimuli might have made a fictional character scared or sad, provided more specific evidence. In particular, most children described the putative monsters as aggressive, ready to pounce, lurking in the dark, equipped with teeth or claws, and other such features of dangerous animals (Bergstrom, submitted for publication). In another unpublished study in our lab, children were presented with accounts of a day at the playground, with the reported presence of either a toy-snatching or an aggressive animal. Although there was no difference in overall memory for the stories (context, location, circumstances), the key details of the animal's appearance were better recalled in the predator-like condition (Boyer and Wilkie, submitted for publication).

The construal of animals (real or not) as potentially threatening is typical of that period (Jones and Jones, 1949). Inexperienced children typically over-estimate the intelligence, detection powers and aggressiveness of animals, attributing great ferocity to sheep and goats. At that age they also acquire fears of quasi-predators from vicarious experience and information (Askew and Field, 2007; Field and Lawson, 2008). Information about such animals triggers attentional focus (Purkis and Lipp, 2007; Waters et al., 2008). This fear target seems to be highly similar in very different cultures, e.g. South Africa (Muris et al., 2008), Nigeria (Maduewesi, 1982), US Native American (Wallis, 1954), and Italy (Salcuni et al., 2009).

Early childhood is also the period at which young children develop an understanding of illness, pathogens and contagion. At this stage, most children have a rudimentary, intuitive understanding of physiological function. They see most illness as the result, not of dysfunction, but of invasion by invisible vectors, even before they learn about local theories of germs or pathogens (Kalish, 1996, 1999). This understanding is the basis for their intuitive distinction between accidents and disease. As a result, children at that age treat most diseases (including e.g. dementia or cancer) as contagious (Bares and Gelman, 2008; Myant and Williams, 2005). This conception of potential contamination or contagion is the basis of some childhood folklore (e.g. the notion that some children have "cooties"), but also of their interest in and rejection of particular substances (e.g. spit, blood, feces) or practices (e.g. kissing) as "yucky".

These early fear-targets are generally present throughout middle and into late childhood (Pintner and Lev, 1940). In addition, this is also a period during which social fears come online (Field et al., 2003; Weeks et al., 2009), together with the appearance of subclinical but also pathological social anxiety (Rubin et al., 2009).

Adolescence is the period at which intense social threats are added to the mix (Kendler et al., 2008; Lane and Gullone, 1999; Sumter et al., 2009). The main change here is not that the fear-targets are different but that their intensity and behavioral effects are much greater. A salient fear-target is loss of friendship, e.g. friends "betraying" one, allying with "enemies", or being less (or less exclusively) committed to one. In adolescence, friendship is more closely associated with social support than in childhood (De Goede et al., 2009; Poulin and Pedersen, 2007). Another major fear-target is status loss, especially in the context of social environments like school that one cannot easily leave. Low status and peer victimization are central fears. They are also good predictors of social anxiety (Siegel et al., 2009). Finally, part of adolescents' social fears focus on competition for romantic success (Bleske and Shackelford, 2001). Again, the developmental pattern seems to be roughly similar in different cultures, see e.g. Liu and Li (2008) for China.

Although some of these developmental patterns vary with experience, social input and cultural environment, the main trends seem remarkably stable. An important question, then, is what developmental perspective can best make sense of both commonalities and differences.

2. Accounts of fear-acquisition

Central to early theories of fear-acquisition were classical conditioning accounts, following which any stimulus could become a fear-trigger, given the appropriate CS/UCS pairing (Watson and Rayner, 2000). The main assumption was that most normal fears as well as pathological phobias would be the result of actual particular encounters with the target stimuli. There were several problems with this account. First, the assumption of equipotentiality (all UCS have the same potential for triggering fear-reactions)

flies in the face of experimental and observational facts (Rachman, 1991). After Garcia's pioneering studies (Garcia and Koelling, 1966), many other lab experiments showed that prior dispositions "filtered" associations and therefore made some UCS better candidates for fear-triggers (Rachman, 1977). Second, most human fears, if acquired at all, seemed to result from vicarious experience or information passed on by conspecifics, which does not qualify as conditioning. Third, fear was difficult to elicit by classical conditioning in humans (Rachman, 1977). Finally, long before doubts were raised about the experimental validity of this account, behavioral observations and evolutionary biology has cast doubt on the standard conditioning account. Many encounters with fear-inducing stimuli, with predators in particular, are lethal – so that prior dispositions to avoid the encounter are the only possible fitness-enhancing pathway.

In response to the problems of the conditioning account, cognitive models like Rachman's emphasize the diverse processes that may lead to the consolidation of fear-responses and their association with classes of stimuli (Rachman, 1991). In particular, Rachman's models emphasized three paths to fear-responses. Beyond classical conditioning, as described above, humans could acquire fears through modeling, that is, vicarious experience – being in the presence of conspecifics who experience the fear and thereby modeling it – as well as conceptual information, e.g. from other people's statements about the fear-target (Rachman, 1991). In empirical studies of fear-acquisition, it turned out that most human specific fears seem to be derived from either information or modeling, not conditioning (see for (Muris et al., 2008)). A large literature confirms the importance of information and vicarious experience (Rachman, 1991). However, such studies mainly rely on self-reports which may not be altogether reliable, as participants have only limited access to their own cognitive functions (Mineka and Öhman, 2002) and in any case often report that they have no specific memory of how the fear was acquired, in the same way as they have no insight in the acquisition of other aspects of semantic memory. Some experimental studies addressed these concerns, showing for instance that demonstrated fear of particular animals, through exposure to human facial expressions, could trigger reliable fear-responses (Askew and Field, 2007).

In any case, a description of possible pathways does not exhaust the cognitive processes engaged. Any association between vicarious experience, or verbal information on the one hand, and fear-responses on the other, requires prior dispositions to, precisely, associate these two elements. Pure contingency or similarity are insufficient, or would trigger a proliferation of irrelevant fears. This is a variation on the common computational problem of associationism. If an adult manifests great fear at the sight of a snake, an unbiased learner may associate fear with any one of the manifest features of the visual scene (tall grass, trees nearby, the setting sun, a snake, etc.) instead of acquiring the relevant association. Weeding out the ever-increasing number of possible but irrelevant associations would soon overload any cognitive system.

This is the main motivation for "non-associative" models (Poulton and Menzies, 2002) following which a host of special dispositions interact provide an initial "repertoire" of fear-targets, such as heights (Poulton et al., 1998) or dangerous animals (Öhman and Mineka, 2001). Debates between "neo-conditioning" and "non-associative" accounts of fear-acquisition reflect broader debates about innateness in cognitive structure (see for instance Elman et al., 1996; Spelke, 1998). Empiricist or associative accounts fail to predict the specificity of associations – why people attend only to some of the many possible associations between stimuli. Conversely, classical innate structure accounts may seem to miss the learning processes involved in developing environment-specific adaptive responses. A proper evolutionary perspective, as we see below, may overcome both kinds of limitations.

3. Fear and precaution in an evolutionary perspective

The models reviewed above did not fully integrate evidence from ethological and evolutionary approaches to animal behavior. However, the processes engaged and in particular the process of acquisition may make more sense once considered as adaptive behaviors in the context of natural selection, which favors the evolution of domain-specific cognitive systems that handle recurrent fitness challenges. This domain-specific view of cognition informed by different principles was first popularized by developmental psychologists (Gelman, 1994) and it has received considerable support from both developmental psychology and the study of highly specific cognitive impairment (Caramazza, 1998). Neuroimaging and cognitive neuroscience are now adding to the picture of a federation of evolved competencies that has grown out of laboratory work with children and adults. This view is supported by a wealth of findings from experimental and developmental psychology, linguistics, neuropsychology, and the neurosciences (Gazzaniga, 1998).

In this perspective, cognitive systems are *learning mechanisms*. Each domain-specific system is specialized in picking up particular kinds of information in the organism's environment. That is, "acquired information" and "genetically specified information" are not a zero-sum system (Barrett, 2005b). On the contrary, organisms (e.g. primates) that can acquire vast amounts of information from their environments need vastly more specified initial dispositions than organisms (e.g. invertebrates) that acquire less. Between species, more learning invariably means more instinct, so to speak. This is particularly important to humans, because throughout evolutionary times they have been faced with rapidly changing environments, with seasonal changes, migrations that require appropriate reactions to new environments.

How does this apply to fear and threat-detection? Although much is forever unknown about ancestral life, we do know enough about the conditions of Pleistocene foragers in a tropical savannah to describe some recurrent fitness threats. In particular, humans should be equipped to deal with the following kinds of dangers:

[1] *Predation*. Humans are particularly weak compared to other great apes. They cannot really defend themselves against big cats or other large mammals. Note that in the category of predators we should include not just animals likely to attack humans, but also large prey (elephants), aggressive competitors (e.g. hyenas, bears), as well as small animals such as snakes and spiders (Gerdes et al., 2009).

[2] *Contagion and contamination*. Humans are threatened by a large range of bacteria, viruses, toxins and contaminants (Franco et al., 2009), specially because humans are food generalists who extract nutrients from practically all sources available. A diverse vegetarian diet imposes a cost in terms of toxin absorption, while generalized meat-eating provides a major source of pathogens (Jew et al., 2009). More recently, animal husbandry has put humans in contact with populations of pigs, dogs, cattle, poultry, etc. Agriculture resulted in large concentrations of population, with the increased pathogen load, as well as increased travel and migrations, favoring the spread of exotic pathogens.

[3] *Status threat*. Humans, more than any other species, depend on information and resources from conspecifics (Tooby and DeVore, 1987). They also create complex social hierarchies and compete for status, resources and mates. This creates a new domain of fitness threats, to do with social exclusion, ostracism (Kurzban and Leary, 2001), status loss (Abbott et al., 2003; Marmot, 2006) or simply the stress of competition (Sapolsky, 2004).

[4] *Conspecific violence*. Attacks from other humans is one major threat to fitness – and seems to have been so continuously through human evolution and into historical times (see Neuberg et al., this issue). Violent episodes include both intra-group conflict (feuds,

attacks, disputes over spouses, etc.) and extra-group tribal (or in the modern context, national) warfare. Humans like other primates are aggressively territorial and in the past have generally used surprise attacks to inflict maximum casualties (see surveys in (Gat, 2008; Keeley, 1996)). In both domains of violence the potential threat to women's fitness is much greater than to men's, as physical violence is more directly detrimental to their reproductive potential, and more importantly because of the menace of rape, an ever-present component of violence against women (Ferraro, 1996).

The effects of all these are documented in the archaeological record, so that it makes sense to consider these as the context of evolution of human threat-detection mechanisms. Besides, many fitness threats are common to ancestral and modern environments – the risk of predation is diminished but that of conspecific aggression is not, the dangers from pathogen exposure and contaminants are just as salient.

An important implication of the evolutionary perspective is that threat-detection systems, as cognitive systems in general, are most likely *domain-specific*. Ecologically valid cues that suggest the presence of predators (tracks, spoor) are not relevant for contaminants, which are themselves different from those indicating rivals or enemies. Even within the social domain, detecting a threat to one's status requires attention to particular behaviors, which would receive a completely different interpretation in the context of courtship. So it makes little sense to postulate a general threat-detection system in human minds. A more plausible picture would comprise many different systems geared to different kinds of threats.

4. Stability and appropriateness of the developmental schedule

As noted above, children do not develop fear-targets in an unprincipled way. On the contrary, specific targets come on-line at different stages of childhood. This schedule is astonishingly stable between children in vastly different kinds of social and cultural environments, ranging from nomadic foraging tribes to large cities. Obviously, encounters with strange people, other animals, contaminants, differ a great deal between environments, so that children come to develop distinctly cultural fears and precautions. However, against this background it is all the more striking that during development children become selectively sensitive to particular aspects of their environments, paying attention, e.g. to unfamiliar conspecifics before other animals, to dangerous animals before contaminants, etc. This suggests that a certain number of fear-targets become relevant as a result of distinct stages of typical development. This in itself would seem to favor one of the several "non-associative" models of fear-acquisition, in the sense that the most frequent pathway to fear in children seems to be, neither information nor experience, but a spontaneous search for relevant threat-related features of the environment (e.g. strange faces, dark corners, space under the bed, etc.) (Poulton and Menzies, 2002).

More specific evidence for an evolutionary form of non-associative account stems from the fact that the developmental schedule is not only stable, but also seems evolutionarily appropriate. Developing fears target actual fitness threats. For instance, stranger anxiety is directed at non-familiar, generally non-kin males. It would seem to be appropriate given the infant's helplessness, the occurrence of infanticide in most primate lineages (Hrdy, 1977), and the disproportionate threat from step-fathers as compared to male kin (Daly and Wilson, 1998). Also, note that stranger anxiety is not connected to the number of actual strangers encountered. Indeed, one can observe the same reaction in small bands of

foragers, where the child very rarely encounters unfamiliar people (Konner, 1972).

At later stages, there begin to appear contextually appropriate fears connected to the child's experience, such as the fear of heights measured in familiar "visual cliff" protocols, which appears at the time infants start crawling. Locomotor experience is required for this fear to appear (Campos et al., 1992). The child's reaction to apparent gaps in the ground is highly specific, as the behavioral response (gestures, avoidance) depend on the child's posture (Adolph, 2000).

As many human societies seem to have practiced late weaning but also early introduction of adult foods (Clayton et al., 2006; Konner, 1972), an added danger may lie in the ingestion of new foods, which may explain the widespread food "neophobia" of young children (Birch, 1990; Cashdan, 1994).

In some cases, the fears seem to focus on situations or objects that may be constitute insignificant or non-existent danger in modern circumstances. More often than not these would have been actual threats in the environments in which our fear-systems evolved. The most familiar example would be the great reluctance of young children to go to sleep on their own, away from protecting caregivers. Fears around bedtime, together with elaborate routines and rituals to assuage that anxiety, are almost universal in modern industrial societies with solitary sleeping arrangements and virtually unknown in the rest of the world (see for instance Javo et al., 2004; Rothrauff et al., 2004). Sleeping in isolation from the group, for nomadic foragers, is indeed a situation of great potential danger, especially from predators (Kelly, 1995).

Threats from predators also provides an explanation for the seemingly irrational, and unprovoked, anxiety about monsters and other such dangerous agents. These are invariably described as lurking in the dark, about to pounce on the child. In our studies, children describe them as having claws, sharp teeth, sometimes as furry, but they seldom provide further details of their appearance. In other words they would seem to correspond to an abstract template of the kind of predators humans encountered throughout ancestral times (Barrett, 2005a).

Later developed fears, again, seem to focus on evolutionarily appropriate targets. Early adolescence, especially in pre-industrial environments, constitutes a gradual transition from parents to peers as a major factor in individual fitness. The challenge of that period is to find a specific social niche and build stable networks of reciprocity. These goals are threatened by gossip, competition, friend- or mate-poaching – all of which would be net depressors of fitness (Hess and Hagen, 2006). This is also the time at which gender-specific fears develop, particularly the fear of sexual assault that is observed in high-school (Beale and Baskin, 1983) and middle-school-age girls (Noonan and Charles, 2009). From that time on, women generally fear assault and other crimes much more than men, mostly because they rightly expect any form of assault potentially to lead to rape (Hilinski, 2009).

To say that the developmental schedule is stable and appropriate does not imply that people can only acquire fears of ancestral objects. Threat-detection is a collection of learning systems, which must precisely adapt to the ecologically and culturally diverse forms that fitness-threats can take. That is why an evolved fear-response to weapons is triggered by modern object like guns (Blanchette, 2006). This is what some described as a continuum of innateness (Marks, 2002), although it may be more helpful in this case to abandon the term "innate" altogether. From the perspective outlined here, both the expectation of highly stable targets (e.g. strange males) and the expectation of highly variable ones (e.g. local contaminants, local social threats, local weapons) are equally part of our evolutionary heritage

In evaluating the predictive power of the evolutionary account, it is also relevant to take into account the "dog that did not bark", in

this case the number of fear-targets that *should* be acquired easily if either a direct experience or an associative account were valid. In the same way as monkeys or humans have difficulty acquiring vicarious fears for flowers, and none for spiders (Öhman and Mineka, 2001), it is notoriously difficult for most children to acquire the notion that cars or swimming pools are physically dangerous, or that cigarettes or alcohol are worse contaminants than many “yucky” substances. Young children in Chicago fear monsters and predators that are quite rare in that city, yet ignore most actual urban threats around them (Maurer, 1965).

5. Potential vs. actual threats

It is striking that most children’s fears occur in situations in which there is no actual direct threat – which may lead us to think that threat-detection systems are hyper-active or simply inaccurate in children. That would be misguided, for several reasons. First, as we emphasized, children’s fears come online at times that correspond to actual dangers in evolutionary contexts. Second, as we will explain presently, children and adults are very similar in that respect, in the extent to which they experience fear for dangers that are not yet part of their immediate environment. Third, and most important, we cannot judge that a biological detection system is “wrong” or “hyper-active” simply because it triggers false alarms. In evolution, the only currency for design is fitness, so that detection systems balance the relative costs of false alarms and misses. Natural selection favors systems that err on the side of caution (hyper-detection) when the cost of false alarms is less than that of misses, and conversely lead to risk-taking when the costs are reversed (Haselton et al., 2006). Given the real but small costs incurred in seeking shelter, attracting a caregiver’s attention, avoiding a particular place, denying oneself what may be nutritious, and other precautionary behaviors, the question is whether engaging in such behaviors by mistake reduces fitness more than failing to detect danger. Since contamination, contagion, predation, rape and murder impose enormous fitness costs, one should expect “hyper-detection” to be highly adaptive in these domains (see also Woody and Szechtman, this issue).

Children’s fears seem to be much more about *potential* than *actual* threats – and this is true of adult fears too, as most of the specific fears we described here *begin* in childhood but remain present, in somewhat modified forms, throughout adult life. This focus on potential situations seems consistent with standard assumptions, notably concerning the distinction between *fear* and *anxiety*. This is often mapped onto the actual vs. potential distinction: “fear is the motivation associated with a number of behaviors [...] on exposure to clearly threatening stimuli. Anxiety [denotes] behaviors that occur to potential, signaled or ambiguous threat.” (Blanchard et al., 2008). The distinction is also supported by pharmacological evidence, as pathologies of imminent danger and anxiety syndromes do not seem to respond to the same treatments (McNaughton and Zangrossi, 2008).

It may be of help here to specify the level at which these distinctions are supposed to be relevant. Elsewhere, we emphasized the difference between actual and potential fitness-threats (Boyer and Lienard, 2006, 2008). The difference is mostly in the time-course of appropriate reactions. Actual threats are such that the organism’s life or integrity is in danger unless they freeze, flee or attack. Potential threats are such that inaction only affects the probability of fitness costs at some future point. This was proposed as an *ecological* distinction. It is only partly congruent to another, *ethological* distinction, between typical fear-responses on the one hand (flee, freeze, etc.) and precautionary behaviors (inspection, avoidance). That behavioral distinction itself may or may not be congruent to *neuro-physiological* differences, in the structures engaged and the

neuro-transmitters involved. We can only create confusion if we insist that the same distinction (fear vs. anxiety) should be found at the phenomenological, behavioral, neuro-physiological and ecological levels.

The development of fear and anxiety in children illustrates precisely this point. When children expect monsters or dangerous animals to lurk in dark corners, they are obviously reacting to (unlikely) potential threats. Children’s reactions include what would traditionally be called anxiety responses (avoiding these situations, seeking help) but also in fear-responses (freezing, panicking, running away). So we cannot simply equate the occurrence of fear/anxiety responses with actual/potential threats. Moreover, the very mention of danger situations, e.g. in stories, can also trigger both types of reactions. Human children are in that respect very similar to human adults, who can experience great fear as a result of recalling or imagining threatening situations. As Woody and Szechtman point out (this volume), humans often respond to “future-present” danger.

Human episodic memory and imagination are supported by a capacity of “episodic simulation” that encompasses both past events and possible future circumstances (Addis et al., 2009) engaging specific neural circuitry (Szpunar et al., 2007). To many scholars, such simulation is a necessary component of sophisticated decision-making in humans (Suddendorf and Corballis, 1997, 2007). As this simulation of past or possible episodes engages perceptual imagery, it may have direct effects on emotional systems, and thereby strengthen or dampen motivation towards particular courses of action (Boyer, 2008). In the domain at hand, one may speculate that imagination of possible outcomes, with distinct imagery, is one of the ways in which human minds can activate fear circuitry in response to potential, not just actual, fitness-threats.

6. Typical development and pathology

In our view, another advantage of the evolutionary perspective is to provide a clearer understanding of the similarities and differences between pathology and typical development. There is, as we mentioned in introduction, only a scant and scattered literature on the typical development of threat-detection. This is all the more striking in domains where children or adolescents develop pathologies, for which we often do not have very specific descriptions or theoretical models for typical development.

There are obviously multiple ways in which threat-detection can be involved in pathology. Among these, we should mention (a) indirect pathways, from the aggregated affects of detecting threats and (b) a direct dysfunction in the calibration of the threat-detection systems themselves.

Fitness-threats can lead to pathology through stress, best understood in terms of *allostatic load* (negative consequences of the physiological changes induced by stressors) (McEwen and Stellar, 1993). Responses to stressors activate in various proportion both the sympathetic adrenal–medullar (SAM) system, involved in fast reactions to direct threat (freeze/flee/attack) and the hypothalamic–pituitary–adrenal (HPA) axis, involved in more long-term adaptation to change. Now the HPA system produces various hormones and neurotransmitters, including glucocorticoids (cortisol in humans) with long-term pathogenic effects (see review in Kloet et al., 1996). Even though the system is generally hypo-reactive until adolescence (Spear, 2000), the same connection as in adults, between intensity or frequency of stressors and poor health outcomes, is observed at elementary school-age (Johnston-Brooks et al., 1998) especially in situation of insecure attachment (Spangler and Schieche, 1998). From an evolutionary perspective, different profiles in physiological reactions to stress may be associated with different behavioral strategies. Comparing evidence from

different species in field and lab observations, Korte and colleagues conclude that the rough behavioral distinction between “hawks” and “doves” corresponds to differential activation of the SAM and HPA systems respectively (Korte et al., 2005). In this sense, even though the anticipation of negative events may result in high cost in the form of anxiety pathologies (Schulkin et al., 1994), such pathological outcome may constitute one end of a spectrum of adaptive strategies.

In some pathologies the detection systems themselves are involved in the symptoms. A salient example is obsessive-compulsive disorder (see Woody and Szechtman, this issue, for more detail on the neuro-physiology of OCD in relation to threat-detection). The etiology of OCD is not entirely clear. In children abrupt onset is often linked to auto-immune reactions, among other instances of “pediatric autoimmune neuro-psychiatric disorders associated with streptococcal infections” (PANDAS) (Mabrouk and Eapen, 2009), with moderate heritability (Gelernter and Stein, 2009). The OCD pathology is often described as discontinuous with the “normal” routines of childhood (Leonard et al., 1990). However, discussion of the normal-pathological demarcation are difficult in the absence of a proper understanding of the condition’s non-clinical counterpart in development, namely the urge to develop routines and rituals in early and middle childhood. Early childhood, starting at age 2, is a period of intense ritualization by children and anxious perfectionism, particularly in the performance of daily routines (Evans et al., 1997, 1999). Other behaviors are often associated with this development, such as intense emotions about “transitional” objects, repetition of particular actions a specific number of times, an interest in lining up or arranging patterns of objects, etc. The tendency to engage in rituals is correlated with trait anxiety and fearfulness (Zohar and Felz, 2001). The themes and the age-range of childhood ritualized behavior are similar across different cultural groups (Zohar and Felz, 2001).

Now childhood and adult OCD are related to early developed threat-detection processes, in the sense that obsessions typically center on such fitness-threats as contamination and contagion, injury, predators or intruders, and social exclusion, while the precautionary rituals are often about washing, cleansing, purifying the body (Boyer and Lienard, 2006, 2008). Also, the fears of OCD follow the developmental schedule identified above. Younger children’s ritualistic behaviors are related to prepotent fears such as stranger and separation anxieties, whereas the ritualistic behaviors of older ones are related to more specific and contextual fears such as contamination and social hazard (Evans et al., 1999). In this context, it would seem that OCD symptomatology constitutes an exaggeration of evolved threat-detection systems, as clinicians and anthropologists have argued (Abed and de Pauw, 1998; Boyer and Lienard, 2006; Szechtman and Woody, 2004).

One could make a similar point as regards the connections between adaptive fears, as described here, and the occurrence of pathological phobias (Hofmann et al., 2004; Nesse, 1998). Classical conditioning accounts derived some of their strength from the therapeutic use of counter-conditioning and habituation (see e.g. Jones and Jones, 1928 for a famous demonstration). But the model was also clearly insufficient, given the restricted range of phobias in most presentations (snakes and spiders rather than cows and rabbits, height rather than length, public ridicule but not public praise), the absence of an experiential pathway to fear-acquisition in most cases, and the clear connection between phobic targets and common fear-targets (Coelho and Purkis, 2009; Öhman and Mineka, 2001). In terms of development, it is clear that at least some aspects of adult phobias are almost identical to childhood fear-cognitions, for instance a focus on the special psycho-physics of snakes in the grass (DeLoache and LoBue, 2009) or the disgust induced by arachnids (Gerdes et al., 2009). Again, it would

seem that most of the computational machinery is the same in clinical and non-clinical presentations, while calibration is different.

7. Outstanding questions

Several developmental issues remain to be addressed, of which the following are only a small selection.

Neurophysiological development. Threat-detection and precaution follow a strict developmental schedule. Although some structures supporting this cognitive domain are fairly well-identified (from neuro-imaging and neuro-psychological evidence, see Fiddick, this volume), there is still no general account of their unfolding during brain maturation. In some domains, like social competence and interaction, it is possible to connect system-level neural development with behavior (Carver and Cornew, 2009; Johnson, 2010) – but even there the processes underpinning threat identification and precautions remain obscure

Evolution and genetics. The (certainly polygenic) genomic substrate and the proteomics of typical development for threat-detection are still a mystery, as is the case for most other neuro-cognitive developmental trends. Also, the existence of pathological exaggeration of the systems’ functions raises the question, whether this exaggeration may itself be the outcome of selective pressure (see Fiddick, this issue). Bradshaw and Sheppard, for instance, point out that a large range of disorders (OCD, PTSD, attention-deficit hyperactivity disorder, Tourette’s syndrome, trichotillomania) are highly co-morbid, affect the same fronto-striatal neural circuitry, and are moderately to strongly heritable (Bradshaw and Sheppard, 2000). Some phenotypes that become pathological in modern environments may have had adaptive value in ancestral ones (Bracha, 2006), see also Korte et al. (2005) and Pine and Shapiro (2006). In particular, “excessive” interest in fear-targets or precautions may have been contextually appropriate (Nesse, 1999). However, it must be noted that these evolutionary models consist largely in retrodiction. They should be completed by predictive hypotheses, which so far is not the case

Cross-cultural and ecological aspects. To the extent that threat-detection systems are learning systems, they should focus on specific aspects of environments, in particular on highly variable aspects of these environments. That is why an integrated perspective on development should make use of information concerning threat-detection in highly different ecological or cultural environments. This is obvious if one consider for instance the important differences in pathological presentation for anxiety disorders between different places, and the importance of “culture-bound syndromes” in this domain (Miranda and Fraser, 2002; Prince, 1993; Stein, 1993). This systematic cross-cultural comparative perspective is largely missing from current accounts of threat-detection development

We do not have a unified account of fear-acquisition and fear-detection (Armfield, 2006), and *a fortiori* their developmental aspects are still largely unknown. In agreement with other specialists (Blanchard et al., 2001; Bradshaw and Sheppard, 2000; Hofmann et al., 2004; Nesse, 1999; Öhman and Mineka, 2001), we assume that biological evolution is the proper background to a unified account in this domain. This however is only a starting point. A major task for research in this domain will consist in identifying the specific computational systems that orient the child’s attention to specific environmental cues for fitness-threats, as well as the developing neuro-physiological systems that govern threat-detection and security motivation.

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