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Chapter 1

THE BEHAVIORAL IMMUNE SYSTEM: HOW DOES IT CONTRIBUTE TO OUR UNDERSTANDING OF HUMAN BEHAVIOR?

Gaëtan Thiebaut[1], Alain Méot[2], Arnaud Witt[1], Pavol Prokop[3,4] and Patrick Bonin[1,*]

[1]Univ. Bourgogne Franche-Comté,
LEAD-CNRS UMR5022, Dijon, France
[2]Université Clermont-Auvergne, LAPSCO-CNRS UMR6024,
Clermont-Ferrand, France
[3]Department of Environmental Ecology,
Faculty of Natural Sciences, Comenius University,
Bratislava, Slovakia
[4]Institute of Zoology, Slovak Academy of Sciences,
Bratislava, Slovakia

* Corresponding Author's E-mail: Patrick.Bonin@u-bourgogne.fr.

Abstract

The aim of this chapter is to present theoretical and empirical arguments in support of the existence of a defense system against pathogens: the Behavioral Immune System (BIS). Complementary to the well-known biological immune system, this system represents a recent theoretical proposition which has given rise to an increasing number of studies. After a description of the functional characteristics of the BIS, we will describe a range of studies on the cognitive (e.g., perception of pathogens, memorization of sources of contamination), emotional (e.g., role of disgust), motivational and social (e.g., discrimination, xenophobia) aspects of this system. In the context of the global pandemic due to the ‘SARS-CoV-2’ coronavirus, we hope to provide an overview of a number of works, rooted in the evolutionary sciences, which strongly suggest that pathogens, which are our evolutionary companions, shape a large number of our psychological behaviors.

Keywords: behavioral immune system, pathogens; disgust, evolutionary psychology

Introduction

For evolutionary psychologists, the biological and cultural aspects of human behavior are not opposed but are instead interrelated (Bonin, 2017; Bonin & Méot, 2019; Buss, 2015, 2019; Pinker, 2002; Steward-Williams, 2018). Evolution did not influence only human morphology, but also the human brain and all the psychological processes and behaviors which are necessarily products of brain activity. Evolutionary psychology is a relatively young discipline which forms the background for the current chapter dedicated to the Behavioral Immune System (BIS).

During its evolutionary history, Humanity has been confronted with a large number of selective pressures (Buss, 2019; Bonin, 2017; for a definition of the concept of "selective pressure," see Bonin & Méot, 2019) in the form of "hostile forces" which have required it to adapt to its environment (Darwin, 1859). Pathogens have constituted one of these pressures. Present on Earth for longer than humans (and also since the appearance of the primates 55 million years ago) (Pin, 2015), these agents (e.g., bacteria, viruses, parasitic worms) have antagonistic relations with their hosts and are capable of causing them harm (Ewald, 1993; Van Blerkom, 1993). We can think of these micro-organisms as "micro-predators," threatening us as lions, tigers or crocodiles might but doing so with the greatest "discretion" since they are invisible to our eyes! However, it should be remembered that not all these micro-organisms are pathogenic and that many of them act as 'collaborators', such as those present in the gut microbiota (Sonnenburg & Sonnenburg, 2016). Nevertheless, among the pathogens, as noted by Barker, Stevens, and Bloomfield (2001, citing Horsfall, 1965), approximately a thousand different types of virus are known for their ability to infect human beings and are responsible for approximately 60% of human infections. As Sastre (2018) explains,

> "Globally, pathogens have constituted and continue to constitute a major adaptive problem for all living organisms – even pathogens have to watch out for pathogens. This is why they are one of the most potent factors of evolution." (p. 53)

Proof of this can be seen in the fact that pathogens have been responsible for more deaths throughout human history than all the other causes together (e.g., wars, accidents, natural disasters) (Inhorm & Brown, 1990), in particular during the numerous pandemics from which humanity has suffered (Raoult, 2020, and Figure 1 for an illustration).

Let us take the famous example of the Bubonic Plague, which was the first (known) plague-type pandemic to affect the western world in the sixth century during the reign of Justinian (527-565 AD) (Vitaux, 2010). Originating in Ethiopia in 541, this epidemic quickly spread through Egypt, Palestine and Syria before arriving in Byzantium in 542. Related to this, epidemics developed in Persia in the East, and also in the West (Marseille in 543, and then spreading to the Mediterranean areas of Spain) before disappearing in 767. This episode was to cause some 100 million deaths (this figure is a matter of debate; however, estimates vary between 25 and 100 million victims). The centuries that followed suffered from further examples of such disasters: the Black Death, the Manchurian plague, and even today, pandemics continue to rage! At the time of writing of this article, the entire world is being ravaged by the SARS-CoV-2 coronavirus, and more specifically by the disease it causes: COVID-19.

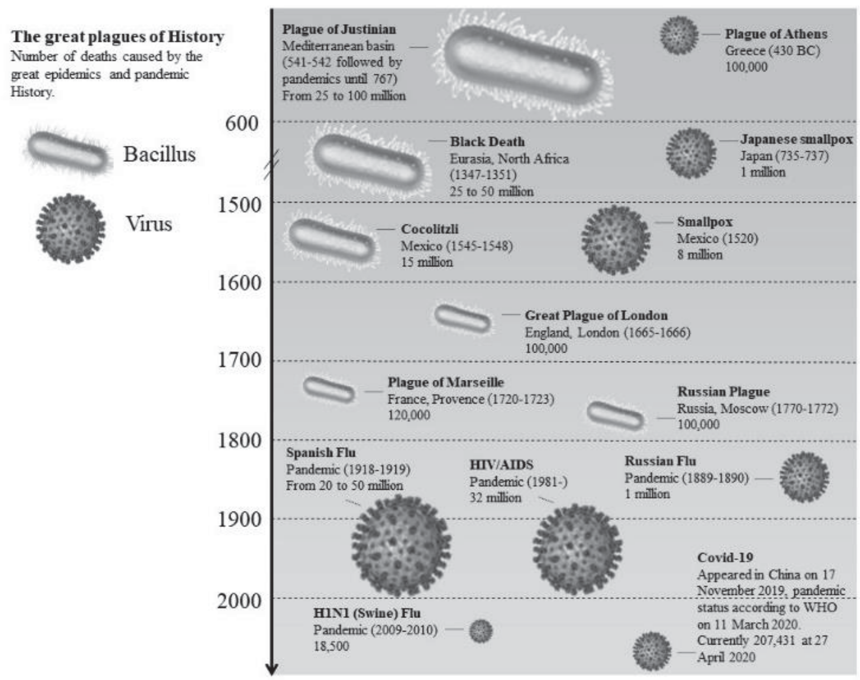

Figure 1. The major epidemics (from Le Point 2486, 16 April 2020, page 59).

Viruses, bacteria, parasites… are present everywhere and all organisms have to cope with them. Thus, in our modern Western societies, bacteria thrive in our homes, public spaces and workplaces alike. As shown by Hewitt, Gerba, Maxwell, and Kelley (2012), of all the types of surface analyzed in the various buildings used for work in the United States, it is the chairs and telephones that are the most contaminated and those used by men are even more so than those used by women, not only in terms of the quantity of viable bacteria but also with regard to the diversity of the bacteria present. Surprisingly perhaps, hundreds of suburban dwellers were tested at bus stops or railway platforms in the United Kingdom and it was found that 28% of them had bacteria of fecal origin on their hands (Judah, Donachie, Cobb, Schmidt, Holland, & Curtis, 2010). This shows the importance of washing one's hands regularly and not only during a pandemic. A recent study conducted in 21 countries (Lin, Liu, & Chiu, in press) has shown that the number of Google searches on the expression "hand washing" (during the period from 18th January 2019 to 18th February 2020) was correlated with a lower speed of COVID-19 transmission (for the period from 19th February to 10th March 2020). This makes clear the importance, in terms of public health, of the effectiveness of messages intended to encourage people to wash their hands frequently (Grant & Hofmann, 2011).

A veritable scourge for humans, and animals in general, pathogens exploit many routes to enter other organisms. As far as human beings are concerned, these access routes into our bodies include the surface of the skin (e.g., hand contact), as well as the nasal and oral passageways. As Raoult (2020) states so succinctly:

> "Humans can transmit microbes between one another by touching, by coughing, via fecal matter that contaminates the hands or through drinking water, through sexual contact, and certain insects or ticks can, when they bite or sting us, transmit microbes that they have contracted elsewhere from a human or another mammal." (p. 155)

If these infectious agents successfully get past these natural barriers (e.g., acidic perspiration of our bodies, tears saturated with antibodies), they must then confront a sophisticated system that is the result of a long period of evolution: the biological immune system (Richtel, 2019; Sompayrac, 2016). This defense system (Farmer, Packard, & Perelson, 1986) comprises an innate immune response (which first detects and then destroys intruders) and an adaptive immune response. With this latter response, destruction takes longer. In effect, the "antigen-presenting" cells must come into contact with a lymphocyte in the lymphatic ganglion and "present" it with an antigen that comes from a pathogen. It is only then that the lymphocyte becomes immunocompetent for the detection of this specific intrusion, multiplies (i.e., clonal amplification) and thus destroys the foreign body. Although the biological immune system is relatively effective, it has a high physiological cost (Schaller & Duncan, 2007). According to Sastre (2018),

> it is a "defensive arsenal which has its overheads: our metabolic demands grow on average by 16% after a vaccine and by 30% during an infection." (p. 54)

Consequently, the resting metabolic rate increases by approximately 13% for each one-degree Celsius rise in body temperature (Schrock, Snodgrass, & Sugiyama, 2020). This physiological cost therefore deprives individuals of energy that could be devoted to other activities such as looking after one's family, going to work, meeting partners, etc. and consequently limits social life. The fight against disease, and its transmission, often obliges individuals to withdraw from social contact. However, numerous studies have shown the potentially harmful effect of social isolation on humans, and of confinement in particular (Brooks, Webster, Smith, Woodland, Wessely, Greenberg, & Rubin, 2020). Social isolation is comparable to a feeling of physical pain (Baumeister & Leary, 1995; Eisenberger, Lieberman, & Williams, 2003; Epley, Waytz, & Cacioppo, 2007), or a lack of food (Tomova, Wang, Thompson, Matthews, Takahashi, Tye, & Saxe, 2020). The biological immune system therefore has the drawback of only combatting the infection once it has been contracted (Allen & Wynn, 2011). It is therefore the last line of defense against diseases. Another sign of adaptation would appear to lie in possessing a defensive system which acts upstream of the biological immune system: this is the BIS which, however, is not specific to humans as a species, as we shall see later. As indicated above, the aim of the present chapter is to present to a wider audience a system that is still (relatively) unknown in psychological circles but which shapes our behavior, as a growing number of studies attest. We shall therefore see that many behaviors are better explained in terms of this concept (Schaller, 2006; Schaller & Duncan, 2007).

HOW DOES THE BEHAVIORAL IMMUNE SYSTEM WORK?

In this section, we shall describe how the BIS works. However, it is important to point out that this theoretical proposal is still the subject of theoretical development and debate (see Lieberman & Patrick, 2018; Lieberman, Billingsley, & Patrick, 2018; Murray & Schaller, 2016) and the current theoretical framework can be characterized as work in progress. This preliminary description will allow readers to better understand the research conducted in accordance with this approach. The BIS concept was originally developed by social psychologists who have studied behavioral aspects such as personal and collective social avoidance. The cognitive orientation of work into the BIS is more recent.

Why Have a Behavioral Immune System?

The ultimate function of the BIS is to prevent us from entering into contact with pathogenic agents. As we have already said, it acts as a first line of defense against disease. At the macroscopic level, the BIS contains three components: cognitive, affective, and behavioral/motivational. Although this division is arbitrary, it is nevertheless useful for describing the system since, in reality, the BIS functions in an integrated way.

The BIS is not specific to the human species and, indeed, we also observe pathogen-avoidance behaviors in the animal realm. For example, mice avoid mating with partners that are infected by parasites (Kavaliers, Colwell, Braun, & Choleris, 2003); tadpoles do everything they can to avoid swimming close to others of their kind that are infected by intestinal parasites (Kiesecker, Skelly, Beard, & Preisser, 1999); the Caribbean spiny lobster flees from conspecifics infected by a lethal virus (Behringer, Butler, & Shields, 2006); grazing animals move away from areas contaminated by fecal matter and prefer to go and graze in "healthier" areas (Brambilla, Von Hardenberg, Kristo, Bassano, & Bogliani, 2013; in mandrills: see Sarabian, Ngoubangoye & MacIntosh, 2020). The aim of all these behaviors is to limit the risk of infection and the propagation of pathogens. In humans, as in animals, the activation of the BIS results in behaviors that permit distantiation from diseased individuals and particularly those perceived as being contagious (Crandall & Moriarty, 1995; Kouznetsova, Stevenson, Oaten, & Case, 2012). In short, the ultimate function of the BIS is to generate avoidance behaviors (Kurzban & Leary, 2001; Schaller, Park, & Faulkner, 2003).

Disgust: An Emotion at the Heart of the BIS

Emotions (e.g., fear, anger, disgust, joy) are adaptive in that they enable us to confront critical life situations; they ensure our survival (Lieberman & Patrick, 2018). For example, if one suddenly finds oneself face-to-face with a bear, fear guides a rapid decision-making process, as in "fight" or "flee" (Seligman, 1971). Numerous studies have shown the involvement of disgust in the avoidance of pathogens (Oaten, Stevenson, & Case, 2009). Indeed, the link between contamination and disgust seems to be all the stronger the greater the risk of the presence of pathogens is, with the result that numerous studies have interpreted the disgust felt by individuals in the presence of certain stimuli as an indicator of pathogens (Troisi, 2020). Consequently, the emotion of disgust is triggered in a variety of situations, for example when confronted with a person of dubious hygiene, a dish that has gone off, or also situations involving deviant sexual practices (e.g., pedophilia, incest). It is widely accepted that disgust has three domains: pathogen-related, sexual and moral (Tybur, Lieberman, & Griskevicius, 2009, see below). Disgust leads to a feeling of nausea and is manifested by a characteristic facial expression (e.g., wrinkled nose, curled lips) (Rozin, Lowery, & Ebert, 1994). Acting as a genuine alarm system, it controls the deployment of distancing behaviors with regard to the source of the contamination. All our senses can lead us to feel disgust and different stimuli are therefore able to cause it. To give only a few examples, *hearing* someone vomiting can cause us to feel nausea and even make us vomit ourselves! A rotting *smell* (e.g., milk that has gone off), blood or fecal matter generally causes a feeling of disgust.

The same happens when foodstuffs no longer fit for consumption are *ingested*, when one enters a dirty toilet, or when one *touches* a viscous substance (Saluja & Stevenson, 2019). Thus, an evaluation of the presence of pathogens must be performed for an avoidance behavior to be initiated and this behavior will or will not be implemented depending on the level of disgust felt.

Disgust: Origin and Role in the BIS

Evolutionary psychology focuses on the ultimate explanations of behaviors without, however, neglecting the proximal explanations (Bonin, 2017, 2018; Bonin & Méot, 2019; Nairne & Pandeirada, 2016). Within the BIS framework; the *original* function of disgust is to protect individuals against ingesting toxins (Curtis et al., 2004; Oaten et al., 2009). Individuals therefore feel disgusted by things that risk contaminating them. But where does the disgust come from? Charles Darwin [1809-1882] described this emotion as "something revolting, primarily in relation to the sense of taste, as actually perceived or vividly imagined." Originally, disgust would have been associated with food (Lieberman & Patrick, 2018) or, more generally, things which should not be eaten. According to Herz (2018),

> "In nature, a bitter taste is habitually an indicator of poison - from toxic berries through to rotten meat - and we naturally dislike this taste." (p. 37)

Indeed, vegetable toxins are bitter and rotten food turns to acid. These two tastes are also found in disease and decomposition (e.g., feces, urine, vomit, putrefaction, etc.) (Hughes & McNab, 2008). However, disgust is not an alarm signal solely with regard to food consumption; it affects all the spheres of everyday life: animals (and, in particular, insects which are vectors of disease such as cockroaches and mosquitos), hygiene (smell of feet, strong body odor), sexuality (sexual relations with family members, animals or children), bodily disfigurements (scars, burns), or the sphere of death (corpse, decomposition) and bodily secretions (sweat, blood, sperm, vomit, feces). These latter are veritable stores of pathogens. For example, a single ml of vomit from a sick person contains approximately 10^7 viral particles and a gram of feces contains approximately 10^{12} (Barker et al., 2001).

Disgust can also extend to behaviors that have no direct link with potential contaminants. Indeed, an observer will feel disgust toward an individual deliberately hitting someone in a wheelchair (Inbar, Pizarro, & Bloom, 2012; Schnall, Haidt, Clore, & Jordan, 2008). In such cases, we speak of co-optation, that is to say that, from disgust, an emotion has been derived which leads to distancing from conspecifics whose social behaviors may be harmful (Chapman, Kim, Susskind, & Anderson, 2009). However, in this article, we shall not address the moral aspects related to disgust (for these aspects, see, for example: Chapman et al., 2009; Inbar et al., 2012; Lieberman & Patrick, 2018; Molho, Tybur, Güler, Balliet, & Hofmann, 2017; Schnall et al., 2008), or the links between political opinions and disgust (for these aspects, see, for example: Helzer, & Pizarro, 2011; Inbar, Pizarro, Iyer, & Haidt, 2012; Liuzza, Lindholm, Hawley, Gustafsson Sendén, Ekström, Olsson, & Olofsson, 2018; Murray, Schaller, & Suedfeld, 2013; Shook, Oosterhoff, Terrizzi, & Brady, 2017; Thornhill, Fincher, & Aran, 2009; White, Kenrick, & Neuberg, 2013). Instead, we will focus on pathogen-related disgust and its relation to disease avoidance or, more broadly, the BIS.

The evolutionary roots of disgust go back a very long way. Indeed, sea anemones (a phylogenetically old species as Chapman et al., 2009 recall) are capable of everting their gastrovascular cavities in response to a bitter substance (Garcia & Hankins, 1975). Disgust is an adaptation (Bonin, 2017) which, as we have already said, makes it possible to put a distance between us and the things that threaten our physical and/or mental integrity. When a stimulus is detected and generates disgust, individuals deploy an aversion and avoidance response. It has been shown that the persons who are most sensitive to pathogen-related disgust introduce a greater distance between themselves and others during their social relations than people who are less sensitive (Park, 2015). To demonstrate this, Park (2015) asked participants to move toward a third person and to stop when they felt that they were at a comfortable physical distance to hold a conversation. The results showed that the average distance was greater for the individuals who were most easily disgusted (disgust was measured by means of a self-administered questionnaire: the "*three domain disgust scale*": Tybur, Lieberman, & Griskevicius [2009], presented below) and those who were the most introverted (this personality trait was measured by means of a personality questionnaire: the "Big-5" (John, Naumann, & Soto [2008]). Keeping a greater distance from other people decreases the risk of contamination, which is why evolutionary psychologists consider these associations to be adaptive.

It should be acknowledged that disgust responses are plastic and at least partly related to environmental conditions. It should be remembered that our ancestors evolved in small groups in the African savanna under frequent threat of starvation (Tooby & Cosmides, 1990). It is therefore reasonable to suggest that hunger could moderate disgust responses. Indeed, hungry people are less disgusted when watching pictures of unpalatable foods than well-fed people (Hoefling et al., 2009). Domain-specific plasticity in disgust sensitivity tolerates the consumption of low-quality food in harsh environments, which is better than risking death from starvation.

How Is Disgust Measured?

Disgust is primarily measured by means of self-administered questionnaires, which can evaluate different dimensions (or fields of application) of disgust, such as that developed by Haidt, McCauley, and Rozin (1994). This questionnaire covers seven domains: food, animals, body products, sex, body envelope violations, hygiene and death. A fine-tuned version of this scale has been proposed in order to reduce it to three domains: "core disgust," "animal reminder disgust," and "contamination-based disgust" (Olatunji, Williams, Tolin, Abramovitz, Sawchuk, Lohr, & Elwood, 2007). Let us take a few items associated with each of these three domains by way of an illustration. For core disgust, we find items such as: "It bothers me to hear someone clear a throat full of mucus," "You are about to drink a glass of milk when you smell that it is spoiled." With regard to disgust related to our animal nature, that is to say disgust regarding things that recall humanity's animal origins, there are items such as "It would bother me to be in a science class and see a human hand preserved in a jar" or "It would bother me tremendously to touch a dead body." Finally, among the items examining contamination-bases disgust, we find: "I probably would not go to my favorite restaurant if I found out that the cook had a cold" or "I never let any part of my body touch the toilet seat in a public washroom."

Tybur et al.'s (2009) scale—known as the *Three domain disgust scale*—consists of three subscales. In it, participants use Likert scales going from 0 to 6 to evaluate how disgusted they are by different statements. These relate to moral disgust with items such as "stealing from a neighbor" or "forging someone's signature on a legal document"; sexual disgust with, for example: "hearing two strangers having sex," "performing oral sex" and, finally, pathogen disgust, with items such as "stepping on dog poop," "shaking hands with a stranger who has sweaty palms." In this new questionnaire, there are no items relating to our animal nature.

It is possible to measure sensitivity to disgust by means of various items in the Perceived Vulnerability to Disease Scale (PVD), which was developed by Duncan, Schaller, and Park (2009). The PVD comprises 15 items, some of which evaluate perceived (individual) infectability and the others (personal) aversion to germs. Certain items on the germ aversion scale are related to disgust and, according to Tybur, Frankenhuis, and Pollet (2014), this subscale is theoretically and empirically linked to the avoidance of pathogens. To illustrate, it includes items such as: "I prefer to wash my hands pretty soon after shaking someone's hand," "I dislike wearing used clothes because you don't know what the past person who wore it was like," "It really bothers me when people sneeze without covering their mouths." More recently, Hartmann and Siegrist (2018) developed a food disgust scale consisting of eight domains: animal flesh, poor hygiene, human contamination, mold, decaying fruit, decaying fish, decaying vegetables, living contaminants. Disgust can also be evaluated by presenting pictures that are thought to arouse this emotion. This is the approach used in the questionnaire "*C-Disgust*" (Culpepper, Havliček, Leongómez, & Roberts, 2018). Pairs of images were created consisting of a healthy version and a disgust-inducing counterpart. For example, a photograph of a steak on a plate and one of the same steak that had gone off. Another example takes the form of a photograph of a bowl of edible Chinese noodles and one of the same bowl with worms in it. The use of images is beneficial in disgust research, because participants' responses are more sensitive than responses on paper-and-pencil tests (Prokop & Jančovičová 2013, J.M. Tybur, pers. comm).

Emotions, like disgust, can be measured using techniques that make it possible to collect psychophysiological (e.g., electromyograph) or neurophysiological data (e.g., EEG, IRM). It has been possible to describe the characteristic facial expression of disgust by recording physical and physiological parameters. This emotion is revealed, in particular, by: the wrinkling of the eyebrows caused by the activity of the *corrugator supercilii* muscle (De Jong, van Overveld, & Peters, 2011), closing of the eyes, constriction of the pupils and the drawing back of the upper lip (increase in the activity of the *levator labii* muscle, which is responsible for raising the upper lip, De Jong et al., 2011), upward movements of the lower lip and the chin, downward movement of the corners of the mouth and, finally, wrinkling of the nose (Vrana, 1993). Studies have shown that fear and disgust activate different brain areas (e.g., Calder, Lawrence, & Young, 2001). The amygdala is a subcortical structure that is involved in the fear circuit and, in particular, in decision-making in response to a threat ("flight or fight" decisions), whereas the insula and basal ganglia (pallidum and putamen) are involved in disgust (Calder et al., 2001) as are other brain substrates (see below: Mataix-Cols et al., 2008). Differences between fear and disgust have also been shown at the level of the involvement of the sympathetic and parasympathetic nervous systems (Kreibig, 2010). The sympathetic nervous system (responsible, among other things, for accelerating the heart rate) is involved in fear, whereas the parasympathetic nervous system—which is antagonistic to the sympathetic nervous system and responsible, among other things, for lowering the heart rate—is involved in disgust (Levenson, 1992; but see also the study by De Jong et al. [2011] revealing a co-activation of the sympathetic system). Many studies have listed the various modifications observed in the parasympathetic nervous system when disgust is induced (Olatunji & Sawchuk, 2005). Thus, heart rate (Rohrmann & Hopp, 2008; Stark, Walter, Schienle, & Vaitl, 2005), blood pressure (Sledge, 1978) and body temperature (Zajonc & McInstosh, 1992) fall when disgust is felt. A decrease in pupil size has also been observed (Al-Omar, Al-Wabil, & Fawzi, 2013). By contrast, skin conductance (Stark et al., 2005) and the secretion of saliva (De Jong, Van Overveld, & Peters, 2011) increase. For example, the study by De Jong et al. (2011) examined numerous parameters such as secretion of saliva, activation of the facial muscles, heart rate and skin conductance. This study made it possible to investigate potential links between physiological responses and individual sensitivity to disgust (measured using a self-administered questionnaire). Some of the participants, who were fitted with electrodes in order to measure the above variables, watched a neutral video (about spectacle manufacture) and evaluated the disgust they felt. They then watched a disgust-inducing video (featuring the "Jackass" team consuming excessive quantities of eggs and milk until they were sick) and evaluated the disgust felt. The disgust questionnaire (Haidt et al., 1994) provided an individual sensitivity score. The results obtained by De Jong et al. (2011) indicated greater activity of the *levator labii* muscle and a reduction in the activity of the *corrugator* muscle, increased skin conductance, reduced heart rate variability, as well as an increase in heart rate indicating the co-activation of the sympathetic system. These data show that the parasympathetic nervous system is involved during prolonged exposure to disgust-inducing stimuli (see also Levenson, 1992; Stark, Walter, Schienle, & Vaitl, 2005), coupled with a secondary activation of the sympathetic system. Surprisingly, no evidence was found of a link between the physiological responses and sensitivity to disgust, with the most sensitive individuals not exhibiting any greater physiological responses. However, functional MRI revealed that, at the neuronal level, the scores for sensitivity to disgust were positively correlated with the activation of brain regions involved in the processing of disgust, such as the anterior insula, the ventrolateral prefrontal cortex, the temporal pole, the dorsal anterior cingulate gyrus, pallidum-putamen, the visual cortex (Mataix-Cols et al., 2008). In other words, the activation in these brain regions was all the higher the greater the sensitivity to disgust was. Many studies have shown that women are more susceptible to feeling disgust than men, as mentioned by Prokop and Fančovičová (2016) (see also Al-Shawaf, Lewis, & Buss, 2018; Fleischman, 2014; Sparks, Fessler, Chan, Ashokkumar, & Holbrook, 2018). However, why should this be? Prokop and Fančovičová (2016) tested various hypotheses concerning the origin of this difference. These hypotheses are all related to Trivers' theory of parental investment (1972) according to which women are more involved in reproduction than men (gestation period, breast-feeding, etc.). Women would be more frightened of pathogenic agents because they can impact their offspring either directly or indirectly, and their higher level of disgust would permit more extensive protection against these invisible threats (Curtis, Aunger, & Rabie, 2004). In line with this analysis, Prokop and Fančovičová (2016) tested the prediction that women with children would be more easily disgusted than those without children. They performed a study among 299 Slovakian women in their twenties who were either without children or, by contrast, had at least one. They evaluated their sensitivity to disgust by means of various tasks (e.g., disgust felt when seeing pictures of disgust-inducing things or animals [e.g., pictures of bodily fluids, mosquitos]). However, contrary to what was predicted, the results showed that the mothers were less sensitive to disgust than the women without children. Certain researchers think that lower disgust in males may be a part of the male reproductive strategy (Sparks et al., 2018). Many more studies will be necessary in order to better identify the reason or reasons for the difference in the sensitivity to disgust of men and women. Finally, a study conducted on twins using the above-mentioned questionnaire developed by Tybur et al. (2009) suggests that the individual differences related to disgust in the fields of morality, sex and pathogens appear to have a genetic basis (Sherlock, Zietsch, Tybur, & Jern, 2016).

To complete this section devoted to the emotion of disgust, it is important to mention that although it is central to the BIS concept, it is not the only emotion involved in providing protection against pathogenic agents. As we have already said, emotions ensure our survival (Lieberman

& Patrick, 2018) and fear is also an emotion that plays an important role in the avoidance of disease (Galoni, Carpenter, & Rao, 2020; Troisi, 2020). As Troisi (2020) puts it:

> "Disgust and fear are two key emotional responses to infection-connoting cues." (p.73)

However, the involvement of fear has undoubtedly been less studied than that of disgust in pathogen-related avoidance behaviors. Future studies should therefore examine the importance of these emotions in avoiding contamination. Nevertheless, there are questionnaires which specifically evaluate the fear of falling ill, such as the Perceived Vulnerability to Disease Scale ('PVD') presented above (Duncan et al., 2009). In addition, according to Troisi (2020), the cues that can trigger fear (diseases) differ depending on the type of affection: in some cases, fear would be triggered by "cognitive" cues such as degenerative diseases (e.g., senile dementia), since they were not a threat to survival in the distant past, whereas in the case of infectious diseases, fear would be rooted in our "emotional brains" since these were an "evolutionary" threat. Further work will be needed in order to determine the extent to which different diseases are reflected by cognitive, affective and behavioral differences.

The BIS and the "Smoke Detector" Principle

The BIS was not selected for the sure and certain detection of the signs of contamination present in the physical or social environment. For a long time, the very existence of pathogens was unknown. Instead, the BIS tends to detect a probability of the presence of potentially contaminating agents on the basis of often imprecise cues. This system therefore attempts to minimize mistakes which could be harmful or even fatal, such as perceiving a highly contagious person as being healthy (Haselton & Buss, 2000).

Many situations illustrate the fact that natural selection favors behaviors which, in the case of uncertainty, minimize the global cost of mistakes (see Bonin & Méot, 2019 for a summary of the various behavioral biases related to evolution). Thus, imagine that you are walking through a forest and that you suddenly see in your path something that looks long and sinuous. If it is a branch and you mistook it for a snake then you will have certainly run away and expended energy needlessly, but you will still be alive! By contrast, if a snake is there and is mistaken for a branch, then it is possible that the perpetrator of the error will no longer be with us! As far as the BIS is concerned, Nesse (2005) compares it to a smoke detector. It is better if a smoke detector issues an alarm in response to signals that do not have harmful consequences (e.g., the smoke coming from a slice of bread in the toaster) than if it generates too few alarms and allows a fire to break out. Like a smoke detector, the BIS is a system that may be activated by superficial signals of illness or by signs that are similar to those of illness but do not derive from it, such as facial port-wine stains (in this latter case, we speak of pseudo-contamination). By contrast, remaining unconcerned when faced with a person who appears to be perfectly healthy when there is actually a high risk of contagion can lead to a "fatal mistake." As a result, the BIS may "overgeneralize."

Studies have shown that persons who deviate from "the normal" on certain dimensions can be identified by the BIS as posing a risk of contamination. Among these, we find persons with facial port-wine stains (*naeveus flammeus*, Ryan, Oaten, Stevenson, & Case, 2012) (this example will be described in greater detail later in this chapter), obese people (Harris, Waschull, & Walters, 1990; Hebl & Mannix, 2003; Park, Schaller, & Crandall, 2007), disfigured people (Shanmugarajah, Gaind, Clarke, & Butler, 2012), people with a mental illness (Lund & Boggero, 2014) or, indeed, elderly people (Duncan, Lesley, & Schaller, 2009). In the field of food, finally, it is possible to be disgusted by things that pose a real risk of contamination, such as a dog poop, but also by the superficial impressions of non-contaminated things, such as a dog poop-shaped chocolate. Thus, in a study conducted by Rozin, Millman, and Nemeroff (1986), strangers were stopped in a public park and were offered a piece of chocolate. They then evaluated (on a Likert scale) their desire to eat another piece. They were then presented with a chocolate in the shape of either a muffin or a dog poop! They then had to evaluate the extent to which they wished to eat each of the proposed items and, finally, to choose which they preferred. Unsurprisingly, the results revealed a lesser appetite for the chocolate dog poop than for the chocolate muffin (even though the participants knew that the two items were made of the same chocolate).

There are inter-individual differences in our immune defenses. The same is true of the ability to avoid pathogens and therefore our vulnerability to diseases (Schaller & Park, 2011). In a study conducted in 2012, Park, Van Leeuwen, and Stephen found that the BIS was more highly activated in response to unattractive persons in those individuals who were most sensitive to disease. It is possible that such persons are perceived as being in poor health and/or as having lower immunity, the adaptive behavior therefore being to avoid them. Although it goes without saying that stigmatization of this sort raises ethical and societal problems, it is important to emphasize that natural selection has endowed us with mechanisms that allow us to pass on our genes to the next generation and that natural selection is amoral (Bonin, 2017). Finally, a recent study has shown that contaminated persons are less liked than those who are in good health (Sarolidou et al., 2020).

Differences also exist depending on the time of life. Let us take the example of pregnant women. During the first three months of pregnancy, the immune defenses are temporarily lowered, thus more easily exposing the fetus and the mother to pathogen-related risks. The feeling of disgust, and food-related disgust in particular, is greater during this phase (Fessler, Eng, & Navarrete, 2005). Fessler et al. (2005) also noted that, during this phase of heightened vulnerability, pregnant women express more ethnocentrism (see also below), which then falls over the following six months as the immune defenses improve. This suggests that the weaker a person is/feels, the more they will reduce their contact with others, and particularly with members of groups that are less close to them, in order to reduce the risk of contamination (Navarette, Fessler, & Eng, 2007).

STUDIES DEVOTED TO THE COGNITIVE PROCESSES INVOLVED IN THE BIS

Perceptual and Attentional Processes

In this section, we shall look at the detection of the signs of contamination. Many infectious diseases cause symptoms which change the facial appearance, which consequently becomes less prototypical. Facial symmetry appears to be used to judge a person's good health and their resistance to pathogens (Jones, Little, Penton-Voak, Tiddeman, Burt, & Perrett, 2001). In line with this hypothesis, it has been shown that individuals who evaluate themselves as being more vulnerable to infections prefer symmetrical faces (Young, Sacco, & Hugenberg, 2011). In the study in question, two faces were presented to the participants (these were the same face in a "normal" version and a "symmetrical" version created using a photo editor) who had to decide which was the most pleasant to look at. Although we are generally attracted to symmetry, this preference proved to be even more marked the more vulnerable to disease the participant considered him- or herself to be. Consequently, symmetrical faces are preferred because they point to good health.

We are able to distinguish ill people from healthy people despite subtle facial variations, as is shown by research conducted by Axelsson, Sundelin, Olsson, Sorjonen, Axelsson, Lasselin and Lekander (2018). The volunteers in a study were injected either with a bacterium (*Escherichia coli lipopolysaccharide,* abbreviated to LPS) which produces an immune response, or with a placebo. Two hours later, they were photographed. Compared to the "placebo" faces, the faces of the volunteers contaminated by the bacterium were rated as being more tired and as having paler skin and lips. These faces were also evaluated as being more swollen and as having redder eyes, flabbier eyelids, and more turned-down ends of mouths. These recognition abilities are crucial for our survival; visual recognition of ill people is fast and “economical” (i.e., it is not physiologically demanding in the same way as an immune system) and allows us to effectively avoid contamination by disease.

When we are ill, our skin color changes: the face becomes paler and less red, whereas the skin on the arms becomes less red and yellowish but darker (Henderson, Lasselin, Lekander, Olsson, Powis, Axelsson, & Perrett, 2017). As a result, faces whose red coloring has been artificially increased are perceived as being in better health because the reddish coloring is associated with greater oxygenation (Stephen, Coetzee, Law Smith, & Perrett, 2009). Given the importance of the appearance of the skin for determining good (as opposed to poor) health, individuals who rate themselves as being very vulnerable to disease greatly prefer (composite) faces whose skin testifies to good health than those who consider themselves to be less vulnerable (Welling, Conway, DeBruine, & Jones, 2007). (The so-called "composite" faces were created from a number of photos of individuals evaluated by independent judges as being in good rather than poor health).

An important element in the management of social interactions, such as approach or avoidance, is the visibility of stigma (Kouznetsova et al., 2012), and the face would be a particularly rewarding place to "collect" 'honest' information about the state of health of the perceived persons. Of the 25 most mortal epidemic diseases in history, 23 have been revealed by certain facial signs (e.g., cutaneous eruptions, nasal discharges) (Ryan et al., 2012). This type of result has also been obtained for postural indicators. In a study conducted by Sundelin, Karshikoff, Axelsson, Höglund, Lekander, and Axelsson (2015), volunteers were injected either with a placebo or with the LPS bacterium. One hour later, the participants were filmed walking in a corridor. The videos were then evaluated by other participants with regard to the injection condition, and the speed of movement was calculated. The results showed that the "infected" persons, who moved more slowly, were judged to be in less good health and more fatigued than the "controls." Consequently, walking speed is affected by the immune response (see also Lasselin, Sundelin, Wayne, Olsson, Paues Göranson, Axelsson, & Lekander, 2020), thus making it possible to detect the presence of a potential infection and adapt one's behavior with regard to persons who are potentially at risk.

In addition to visual and postural signs, there are also olfactory indicators of illness. In a study designed using the same principle as those presented above, the smell of T-shirts was evaluated following the injection of either the LPS bacterium or a placebo. This smell was judged to be more intense and unpleasant and to evoke poor health (evaluation on Likert scales) following injection of the bacterium (Olsson, et al., 2014) than after injection of a placebo. Similarly, young women judge the smell of young men suffering from gonorrhea as being more unpleasant than that of healthy young men (Moshkin, Litvinova, Litvinova, Bedareva, Lutsyuk, & Gerlinskaya, 2012).

One major problem posed by certain pathogens is that they can be present in some individuals without their hosts showing any visible signs of this (i.e., in the case of individuals who are described as 'asymptomatic'). These individuals cannot therefore be identified as potential threats. In the case of the current pandemic associated with the coronavirus SARS-CoV-2, one formidable problem seems to relate to the asymptomatic carriers (Dezecache, Frith, & Deroy, 2020). Thus, these researchers write:

> "This imperceptibility means that it is not even detected, let alone recognized as a collective threat. Hence, the defensive avoidance mechanisms associated with fear and disgust will not operate." (p. R2)

It is possible that at least certain pathogens (as is hypothesized for SARS-CoV-19) increase the host's activity levels and reduce the feeling of sickness during times of peak transmissibility, consequently increasing transmission rates (Seitz et al., 2020). It should be noted, however, that a substantial number of Caribbean spiny lobsters (*Panulirus argus*) avoid conspecifics that are infected with a lethal virus before any symptoms of the disease emerge (Behringer, Butler & Shields, 2006).

Still in connection with perceptual aspects, albeit at a more global level, Wang and Ackerman (2019) found that when the threat of contamination was induced in individuals, those who had a pronounced aversion to pathogens perceived places that generally had a high social density (e.g., metro, bus, concert hall) as being even more crowded. This perceptual mechanism would be adaptive because entering crowded places would increase social contact and therefore the possible transmission of pathogenic agents. This tendency to "amplify the crowd" would allow persons who are frightened of becoming ill to avoid such places even more effectively and, ultimately, it could protect them against potentially harmful contacts.

The BIS could also have an impact with regard to the perception not of others but of oneself. Ackerman, Tybur, and Mortensen (2018) have shown that, in situations in which the threat represented by pathogenic agents could be made salient (compared to a situation in which no such threat was present), the individuals who had a pronounced aversion to germs were very preoccupied by their physical appearance, with the result that they were more inclined to buy cosmetic face products or consider cosmetic surgery in order to try to improve their physical appearance.

In addition to being perceptually sensitive to the subtle signs of disease, the BIS also controls the allocation of attention. Generally speaking, things that provoke disgust or fear are the object of an attentional bias, that is to say that they are processed before other things (e.g., localized more quickly in space) (Perone, Becker, & Tybur, in press). Studies have shown that disgust-inducing stimuli hold the attention for longer than neutral stimuli (e.g., Charash & McKay, 2002 in a Stroop-type task; Chapman, Johannes, Poppenk, Moscovitch, & Anderson, 2013 in a line discrimination task; Ciesielski, Armstrong, Zald, & Olatunji, 2010 in a target detection task). Directly related to the question of disease, it has also been demonstrated that our attention remains focused for longer on potential signs of disease and shows a certain inertia in moving away from them (Ackerman, Vaughn Becker, Mortensen, Sasaki, Neuberg, & Kenrick, 2009). In the study by Ackerman et al. (2009), the participants saw either healthy faces or faces that differed morphologically (port-wine stain or squint). A geometrical shape was then displayed on the screen (a square or a circle) and the participants had to press a key on the keyboard as quickly as possible to indicate the displayed shape (see Figure 2 for an illustration of the experimental method).

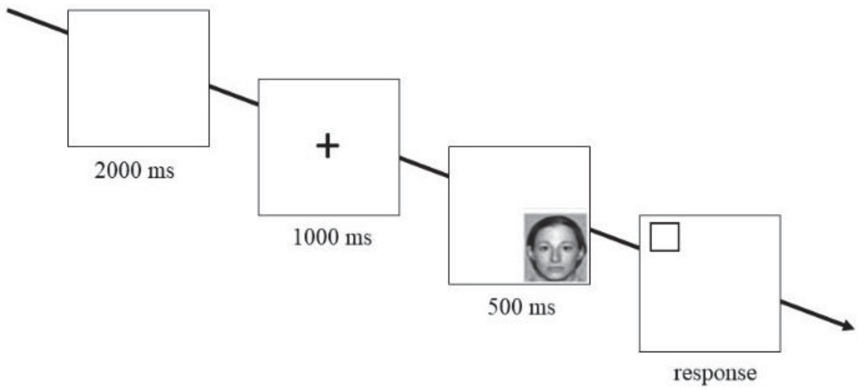

Figure 2. Illustration of the experimental technique used by Ackerman et al. (2009) (from Ackerman et al., 2009, p. 480).

The reaction time taken to judge the shape was then measured and taken as an indicator of attentional disengagement from the target. The results showed that the "disfigured" faces captured more attention than the healthy faces. In effect, the participants found it more difficult to disengage visually from this type of face and therefore took longer to categorize the geometrical shape.

Perone et al. (in press) studied the attentional biases associated with the motivation to avoid pathogens depending on whether this had been provoked experimentally (by means of a disgusting smell (= smell of feces) compared with a smell of peppermint or a neutral smell) or had been identified on the basis of individual characteristics associated with disgust (sensitivity to disgust was evaluated using questionnaires). These researchers used the attentional blink paradigm in which the participants have to detect two target stimuli (e.g., two letters) while other stimuli (e.g., numbers) are scrolling past them very rapidly (for example, every 100 ms). In this way, it is possible to manipulate the position in the series, and therefore the time, of target No. 2 (T2) relative to target No. 1 (T1). Performance on the detection task makes it possible to evaluate the time necessary to disengage the attentional resources devoted to the processing of T1 in order to process T2. An *attentional blink* occurs when T1 is correctly identified whereas T2 is missed. Perone et al. (in press) modified this method in such a way that the T1 targets corresponded to pictures that evoked an emotion (disgust [e.g., dirty toilets]; fear [e.g., aggressive animal]) or that were neutral (e.g., a cup), whereas the T2 targets corresponded to pictures of buildings that had been rotated through 90° to the left or right. Between T1 and T2, the pictures of the buildings were presented in their canonical position. The participants' task was to detect, as quickly as possible, each picture that had undergone a 90° rotation. The interval between T1 and T2 was manipulated (200 ms, 500 ms or 800 ms). The results showed that the disgust-evoking stimuli (T1) produced a greater attentional blink than the neutral stimuli at 200 ms and, interestingly, that the disgust-inducing stimuli provoked a greater attentional blink at 200 ms and 500 ms than the fear-inducing stimuli. The fact of whether disgust was induced (by means of a smell) or resulted from an individual sensitivity to disgust did not modulate these effects. This pattern of results is very interesting since it suggests that the early attentional processing of stimuli that are vectors of pathogens is implemented independently of the context in which these stimuli are perceived. Equally, the researchers suggest that threats linked to pathogens require greater attention on the part of individuals since they need to collect more information in order to evaluate the probability that pathogens are present in the environment. The study by Perone et al. (in press) is therefore highly instructive about the way attention is mobilized in the BIS.

The Memory Processes

The research into the relation between memory and contamination is relatively recent (Bonin, Thiebaut, Witt, & Méot, 2019; Fernandes, Pandeirada, Soares, & Nairne, 2017; Gretz & Huff, 2019; Nairne, 2015). More generally, these works fall within the theoretical framework of adaptive memory (Bonin & Bugaiska, 2014; Nairne, 2010, 2014, 2015, 2016). According to this approach, memory has been shaped by selective pressures in order to respond to survival-related demands (Bonin, Thiebaut, Prokop, & Méot, 2019; Nairne & Pandeirada, 2008) such as protecting oneself against predators or climatic conditions, finding food or, indeed, avoiding disease. The idea of adaptive memory is based primarily on three types of argument, namely the survival effect[1] (e.g., Nairne, Thompson, & Pandeirada, 2007), the animacy effect[2] (e.g., Bonin, Gelin, & Bugaiska, 2014), and the contamination effect (Bonin et al., 2019; Fernandes et al., 2017; Gretz & Huff, 2019; Nairne, 2015). This latter effect corresponds to the fact that we are better able to remember contaminated than uncontaminated things. To demonstrate the presence of a contamination effect in memory, Fernandes et al. (2017), for example, showed adults drawings of everyday objects (e.g., an umbrella, an apple, a fork) which they had associated with faces (or verbal descriptions) which were either healthy or ill (e.g., eczema, conjunctivitis, cold sores). Depending on the study, the participants had either to explicitly remember the associations (Fernandes et al., 2017) or to rate the unpleasantness of touching the object associated with the face of the person who had already touched it (Bonin et al., 2019). After a few minutes spent performing a distractor task, the participants had to recall the names of as many objects as they could independently of the faces. The procedure used in this type of experiment is illustrated in Figure 3.

Globally, the results showed that the objects associated with ill faces (or associated with descriptions indicating that the person was ill) were recalled better than those associated with healthy faces/descriptions. In certain experiments, the source of the contamination was also modified. For example, instead of faces, the experiments made use of hands depicted as being healthy or affected by a highly contagious disease (Gretz & Huff,

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[1] The survival effect corresponds to the fact that information is memorized better when participants are placed in a survival context than in a context not associated with survival (Bonin & Bugaiska, 2014; Bonin et al., 2019; Nairne et al., 2007).

[2] The animacy effect corresponds to the observation that animate entities (e.g., baby) are memorized better than inanimate ones (e.g., mountain) (Bonin, Gelin, & Bugaiska, 2014; Bonin, Gelin, Laroche, Méot, & Bugaiska, 2015; Gelin, Bugaïska, Méot, & Bonin, 2017; Nairne, VanArsdall, Pandeirada, Cogdill, & LeBreton, 2013; Popp & Serra 2016; VanArsdall, Nairne, Pandeirada, & Blunt, 2013).

2019). However, it seems that the memory component of the BIS only becomes active when the threat of contamination is real. Indeed, in one of their experiments, Fernandes et al. (2017) presented faces (healthy versus ill) associated with objects; however, for the faces showing signs of contamination, the participants were told that the "ill" persons were actually actors made-up to appear in a medical series (for example, a series such as "Grey's Anatomy"), whereas the healthy faces were presented as those corresponding to the viewers of the series. No benefit was observed for the memory of the objects associated with the made-up faces compared to the "healthy" faces (Fernandes et al., 2017). The contamination effect therefore no longer seems to emerge when the risk of contamination is not real. However, there are still too few studies on this subject for us to be able to determine exactly what role is played by fear of contamination and/or that of disgust in the contamination effect in memory.

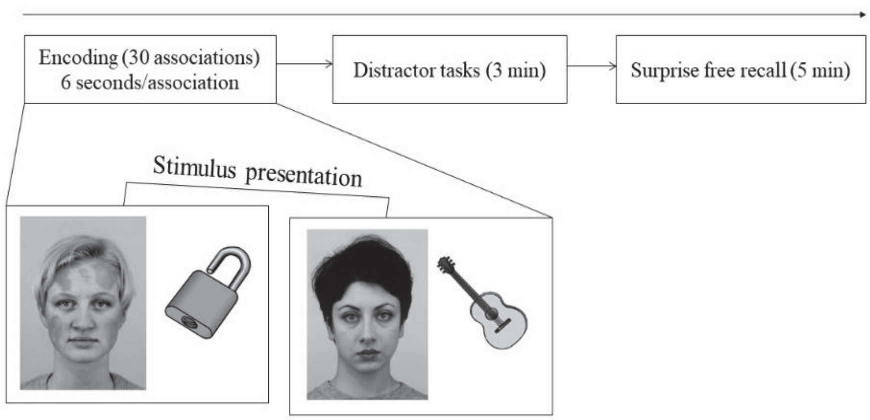

Figure 3. Illustration of the experimental procedure used by Bonin et al. (2019).

How Does the BIS Shape Our Social Behaviors?

As explained above, the BIS was originally a theoretical proposal developed by Schaller (Schaller, 2006; Schaller & Duncan, 2007), a social psychologist, many of whose works therefore relate to issues such as discrimination or conformism. In this section, we have decided, for reasons of clarity of presentation, to illustrate how the concept of the BIS sheds light on certain social behaviors by first examining the individual level ("micro-social" aspects) and then the level of societies and cultures ("macro-social" aspects). However, this division is somewhat arbitrary since these two aspects are interdependent, with certain individual behaviors having consequences at the social level and *vice versa*.

"Micro-Social" Aspects

In this section, we shall consider the individual dimension of social aspects. Being in contact with others can bring us many advantages, such as social opportunities at the romantic or professional levels, and also helps strengthen social ties and thus avoid social isolation. However, pathogens are mostly transmitted via human relations through direct (e.g., handshakes, penetrations during sexual relations) or indirect contact (e.g., water droplets coming from the mouth when we speak, spit). Thus, the denser our environment is in terms of social relations, the more we risk exposing ourselves to pathogens, which explains why during a pandemic, social contact is more or less rigorously restricted. It has been shown that the more vulnerable we consider ourselves to be to disease, the more disgust we express and the more our circle of acquaintances is limited to our close family and friends (Duncan, Schaller, & Park, 2009). Consequently, the vulnerability to disease and the risk associated with the threat of pathogens may generate stigmatization behaviors, in particular towards those who are different from us. This discrimination is expressed in the form of distantiation behaviors. Thus, one hypothesis is that the more ill a person seems to us, the more inclined we will be to reject that person socially (Crandall & Moriarty, 1995). In one study, participants rated diseases on different dimensions (e.g., common versus rare, hereditary versus non-hereditary) and, using a social distance questionnaire, the researchers obtained a score which reflected these participants' propensity to reject others socially. The results showed that the more severe the disease was, the greater the level of expressed social rejection. It is indeed adaptive to distance ourselves as far as possible from individuals who represent a major risk for our health. However, as explained above, the BIS is an imperfect system which is calibrated to detect the presence of pathogens in a probabilistic and sometimes biased way (Wang & Ackerman, 2019). In a context of uncertainty, it can overreact in order to minimize the costs associated with detection errors (Haselton & Nettle, 2006). Consequently, the BIS can trigger avoidance and/or aversive reactions even when the perceived signs are superficial and are not related to disease. Ryan et al. (2012) decided to examine the question of whether a port-wine stain can trigger the same emotional and behavioral responses as an infectious disease such as influenza. Participants had to handle objects (e.g., a diving mask, a harmonica) that had already been touched either by a person in good health or by someone with the 'flu or someone with a port-wine stain. The level of contact between the person and the object was variable (no contact, hand contact, head contact, or mouth contact). In order to depict these prior touching activities, the participants watched a video of the person in question (healthy, ill, or with a port-wine stain) handling the objects and had to imitate their movements. The degree of avoidance of the object and the expression of disgust exhibited by the participants were evaluated. The results showed that in the case of oral contact (e.g., moving the object to the mouth), the participants expressed the same avoidance and disgust reactions for ill persons as for those with a port-wine stain. Consequently, the BIS generates the same aversion and avoidance reactions for a "pseudo-contamination" as it does for a real contamination. These reactions have also been observed, sometimes virulently, towards disfigured individuals, especially when the person making the judgment is highly susceptible to disgust (Shanmugarajah et al., 2012). Other categories of persons also activate discriminatory behaviors, such as mentally ill persons (e.g., obsessive-compulsive disorders, schizophrenia) (Lund & Boggero, 2014), or obese persons (Park et al., 2007). These latter individuals are judged to be more disgusting, less attractive, and more unpleasant than persons with a normal BMI, even though they are not objectively contagious.

It has been observed that discrimination towards persons suffering from an illness (and the disgust felt towards them) is reduced in the case of close friends and family. Indeed, bodily secretions, lack of hygiene and deformities are perceived as being less disgusting when they are associated with relatives, friends or partners, or indeed even with acquaintances, than when they are associated with complete strangers (Peng, Chang, & Zhou, 2013). Similarly, mothers are less repelled by the fecal matter produced by their own babies than that of babies whom they do not know (Case, Repacholi, & Stevenson, 2006). Finally, the disgust expressed in questionnaires as well as at the level of the physiological correlates (fall in heart rate) when faced with disgust-inducing things (e.g., mold, feces) are, like the avoidance behaviors, clearer when associated with unknown persons than with close friends and family (Peng et al., 2013, see also Tybur, Lieberman, Fan, Kupfer, & de Vires, in press).

Discriminatory behaviors can also take the form of xenophobia. When threatened by pathogens, people express more xenophobic attitudes (e.g., Faulkner, Schaller, Park, & Duncan, 2004; Navarrete & Fessler, 2006). As described above, pregnant women have a more ethnocentric attitude during the first three months of pregnancy, that is to say during the period when they and the fetus are the most vulnerable to infections, than later on in pregnancy (Navarrete et al., 2007). In a study (Faulkner et al., 2004), Canadian participants had to look at pictures relating to a threat from pathogens or associated with another threat (e.g., car accidents). They then had to read a short text propounding the idea that Canada is a favorable destination for immigration. The participants' task was to distribute budgets (as a percentage) to eight countries (whose inhabitants might emigrate to Canada) in order to help them enable their citizens to come. Four were considered as being familiar to Canadian participants (Taiwan, Poland, Scotland, Iceland) and the other four as being unfamiliar to them (Peru, Brazil, Mongolia, Nigeria). The results indicated an equal allocation of the budgets in the "accidents" condition, but an unequal distribution in the "pathogens" condition (62% for migrants from familiar countries versus

38% for those from unfamiliar countries). Similarly, another study (Laakasuo, Köbis, Palomäki, & Jokela, 2018) examined the reactions of persons confronted with a hypothetical humanitarian crisis involving a risk of contamination. The data showed that the persons most sensitive to contamination preferred to help the victims by sending money rather than by offering help that committed them more personally, for example by housing the victims. Sending money to the victims does not involve any social contact whereas housing refugees necessitates a contact which increases the risk of contracting the disease. Sensitivity to disgust at body odors (rated by means of a questionnaire) is also positively linked to negative attitudes towards a (fictional) group of strangers (e.g., Zakrzewska, Olofsson, Lindholm, Blomkvist, & Liuzza, 2019). To summarize, all of these studies point in the same direction: as soon as we are threatened by viruses or bacteria, we adopt distancing behaviors with regard to persons who seem to be different from us in order to limit the risk of infection.

Another type of behavior that has been widely studied in the field of social psychology is conformism. In a study conducted in 2012 by Wu and Chang, this behavior was evaluated using works of art. Participants were assigned to one of three experimental conditions. They saw pictures relating to either contamination or accidents or were shown neutral pictures. They then had to rate 30 works of art on Likert scales. Next to each picture, they saw an average score attributed by a group of students similar to themselves. Conformity was then measured by calculating the difference between the average rating (the one indicated next to each work) and the score attributed by the participant. The results showed that when contamination had been used as the prime, the awarded score was closer to that of the group mean than was the case in the other two conditions. This indicates a higher level of conformism after a fear of disease has been induced. In order to adhere to the ideas and opinions of others or imitate their behavior, it is necessary to have confidence in them. However, the individuals who are most disgusted when confronted with pathogenic agents are those who have the least confidence in others, whereas the least disgusted individuals exhibit a higher level of confidence in others (Aarøe, Osmundsen, & Petersen, 2016).

Macro-Social Aspects

Pathogens are therefore able to have a fairly profound impact on our collective behaviors and our ways of life. As suggested by certain studies that we shall present in this section devoted to macro-social aspects, a society's norms and values, the intercultural differences regarding these norms and values, customs and traditions, and indeed the different political systems observed throughout the world (although we shall not examine this latter aspect), appear to be shaped in part by the presence, and in particular the density, of these "micro-predators."

The various regions of the world differ greatly on this dimension and some of them are more heavily impacted than others. For example, regarding malaria, the report by the World Health Organization (WHO) of 19th November 2018 (https://www.who.int/malaria/media/world-malaria-report-2018/fr/) lamented the existence of 219 million cases worldwide in 2017 (92% of which were in Africa) and 435,000 deaths that same year (93% in Africa). Since the prevalence of pathogens is not the same depending on where one is on the planet, numerous studies have suggested that different populations have adopted behaviors and strategies to limit the risk of infection. Let us take the example of food, and more specifically the use of spices in cooking. Many people add a little salt to their potatoes, pepper to their meat, some herbs here, some berries there. But what link can there be between spices and contamination? Spices have antimicrobial properties (Sherman & Billing, 1999): garlic, onions and allspice are the most "deadly" trio for bacteria! Interesting correlations have been reported by Billing and Sherman (1998). The hotter the country (meaning that the proliferation and growth of pathogens is higher), the more highly spiced the food is. India and Malaysia have very spicy foods, whereas this is not the case of Finland and Sweden. Similarly, one study examined 2129 traditional cooking recipes (taken from 107 books) from 36 different countries and showed that meat was eaten with more spices than vegetables are (Sherman & Hash, 2001). At the same time, meat goes off more quickly than vegetables. These data point to an "antimicrobial" use of spices. The method of preparing food is therefore not simply the result of gastronomical preferences but is also undoubtedly dictated by the presence of pathogens.

In general, avoidance behaviors are more prominent in regions which have been historically affected by disease, as a certain number of studies have indicated. For example, Hamamura and Park (2010) conducted a study of persons coming from East Asia (a region with a historically high prevalence of pathogens) and West Asia (a region with a historically lower pathogen prevalence),that is to say, two regions in which health at the national level was comparable in 2009 (period during which swine flu was in decline). The participants had to read an article taken from Wikipedia on seasonal flu and then answer a number of questions regarding worries concerning the risk of infection of people close to them (e.g., friends, family), strangers (e.g., migrants), and concerns relating to the idea of travelling abroad while diseases were present. In general, the East Asians expressed more concern about these three aspects, and even more so regarding foreigners. Data provided by the Airports Council International (ACI (www.airports.org), an organization which monitors air passenger traffic in various parts of the world) have shown that during the period in which swine flu was at its height, air traffic in the Asia-Pacific region fell considerably compared to the West (Europe and North America), with fewer passengers being reported. Similarly, traffic in East Asia fell compared to the situation in the West of the continent.

This does not mean, however, that peoples in regions with higher pathogen prevalence are generally more disgust-sensitive than those living in areas with lower pathogen prevalence. Results from a study surveying 11,501 participants across 30 nations showed that scores on national parasite stress significantly relate to traditionalism, but very weakly to disgust sensitivity (Tybur et al., 2016). Similarly, religious diversity is positively related to parasite stress (Fincher & Thornhill, 2008). These results suggest that adherence to traditional norms and out-group avoidance reinforce barriers between social groups and ultimately reduce parasite transmission (Thornhill & Fincher, 2014).

Personality traits vary in terms of their distribution in different parts of the globe as a function of the prevalence of infectious diseases (e.g., malaria, leprosy, typhoid, tuberculosis), with places that are highly affected by infections being associated with lower levels of extraversion, openness to novelty, and sociosexuality (i.e., desire to have sexual relations without commitment) (Schaller & Murray, 2008) since these personality types are associated with lower numbers of social contacts and therefore with a reduced probability of contracting diseases. The researchers formulated various hypotheses, which are not mutually exclusive, to explain these tendencies. One hypothesis is that in the parts of the world in which infectious diseases are widespread, natural selection has favored alleles associated with certain personality types (e.g., extraverted personality). Another hypothesis is that the genes associated with personality are differentially expressed. Finally, one last hypothesis, which can be thought of as socio-cultural in nature, is that standards, values and behavioral demands differ depending on the prevalence of pathogenic agents and that they shape personality. Other research, such as that conducted by Duncan, Schaller, and Park (2009), has studied the possible links between personality and fear of diseases. The results reveal correlations between aversion to germs and personality traits such as extraversion, neuroticism, and openness to new experience. These results have been confirmed by a recent meta-analysis by Oosterhoff, Shook and Iyer (2018). This study analyzed the data of 32,000 participants taken from 21 studies. The avoidance of diseases correlated most strongly with neuroticism, followed by conscientiousness, openness to new experience, and extraversion. Only agreeableness was not correlated with the avoidance of pathogenic threats. Interestingly, and with regard to the lower expression of openness to new experience, one study showed that technological innovations were also impacted by pathogen prevalence (Murray, 2014). More precisely, Murray (2014) revealed a negative correlation between microbial threat and technological innovation (i.e., number of Nobel Prize winners, patents lodged). Thus, the more a region has been exposed to the threats related to pathogens, the lower the occurrence of technological innovations. This link could be underpinned by conformism and collectivism, which are also known to be higher in regions threatened by infectious agents. Murray, Trudeau, and Schaller (2011) showed that the parts of the world which have historically experienced a high prevalence of pathogens are characterized by social standards that encourage conformism (see also: Chiao & Blizinsky, 2010; Pazhoohi & Luna, 2018; Wu & Chang, 2012). However, how is it that conformism is better able to take root in places that are most severely impacted by pathogens? One proximal explanation is that the alleles linked to a propensity to social conformity have proliferated more in populations with a high pathogen prevalence. One candidate allele is 5-HTTLPR (Chiao & Blizinsky, 2010). At the same time, the parts of the world where there is a lower pathogen prevalence are also those where the most non-conformist behaviors are found, for example in the form of "non-conformist" music styles such as heavy metal. Pazhoohi and Luna (2018) thus report that there are fewer heavy metal groups in the regions (of Europe) that have a high prevalence of pathogens. It would thus seem that musical preferences are also (at least in part) shaped by pathogens!

To summarize, this body of data taken together supports the general hypothesis that lifestyles (e.g., degree of conformism, respect for traditions) vary depending on geographical region, partly due to the recurrent threat linked to pathogens (Murray, Trudeau, & Schaller, 2011), as well as being a reaction to the "brutal" emergence of pandemics as the longitudinal data on the coronavirus pandemic suggest (Rosenfeld & Tomiyama, 2020). Interestingly, these recent data show that, during the pandemic compared to before its appearance, American participants report a higher level of conformism regarding traditional gender-related roles. However, the correlational nature of the results of these various studies demands caution, suggesting that we should not assume a direct causal link between the "presence of pathogens" and "different sociocultural characteristics."

BIS and the Biological Immune System: How Are They Related?

Short Comment on the Biological Immune System

The biological immune system is a set of defenses which make it possible to dissociate between the self and the non-self and destroy any foreign bodies (Richtel, 2019; Sompayrac, 2016). Both inherited and autonomous, it develops over the course of our interactions with pathogenic agents (Conover, 2015). To protect itself against external aggressions, the body possesses two types of mechanism to combat pathogenic agents: innate immunity and acquired immunity. Innate immunity comprises two lines of defense. The external line of defense consists of physical barriers (e.g., the skin and mucous membranes) which form an interface between the environment and our internal constitution. The natural acidity of the epidermis constitutes an environment that is hostile to bacteria (Madison, 2003). If the pathogens make it past these physical and chemical barriers, they are confronted by the internal line of defense. This is activated rapidly as soon as intrusion is detected and reacts non-specifically, that is to say that it is independent of the infectious agents (Medzhitov, 2007). The most common response at this level is inflammation (Gaubert, 2018). This reaction is provoked without knowing the nature of the aggressor. The vasodilatation that it causes permits an increase in the incoming blood flow and the arrival of phagocytes (white blood cells that are able to destroy pathogens). Next, if inflammation has not been sufficient, a second type of defense mechanism is mobilized: adaptive immunity (Bonilla & Oettgen, 2010). This makes use of white blood cells that are specific to vertebrates (B and T lymphocytes or cells) and are able to respond specifically to each type of antigen. In principle, there are in our bodies as many types of antigen as there are types of lymphocyte. The B lymphocytes are in the minority and possess specific receptors which allow the ones that have been activated to secrete antibodies that are responsible for destroying pathogens. The T lymphocytes that are exposed to infectious agents are divided into two categories: the cytotoxic T lymphocytes and the T helper lymphocytes. The first of these destroy cells that are infected with pathogenic agents, while the second stimulate the B lymphocytes, which then produce more antibodies and memory cells which permit immunological memory (Crotty, 2015). It is for this reason that we rarely fall ill twice with the same complaint. Immunological memory permits the rapid reactivation of the defenses responsible for destroying pathogens (Farmer et al., 1986). Alongside this immune system, as described throughout this article, we have the more psychologically-oriented BIS, with its emotional, behavioral and also cognitive components. However, even though they differ in their constitution, these two systems are capable of "collaborating" to confront the risk of pathogens.

Interactions between the Biological Immune System and the BIS

The two immune systems—biological and behavioral—are not mutually exclusive. On the contrary, they have a complementary relationship. It has been shown, for example, that activation of the biological immune system (e.g., due to a recent illness) increases the activity of the BIS (Miller & Maner, 2011). In their study, Miller and Maner (2011) re-used the task developed by Ackerman and co-workers (2009) described above. The participants saw disfigured or normal faces in order to test their attentional bias. Two groups were formed: a first whose members had recently been ill and a second one in which this was not the case. The results then revealed longer reaction times in order to judge whether the shape was a square (versus a circle) for the disfigured faces in the "recently ill" group. In a second study, the normal and disfigured faces were again presented and the participants had to push or pull a joystick (indicating avoidance or approach towards the target, respectively). The recently ill persons were faster than the others in avoiding the disfigured targets. It should be noted that the results of these studies are still undergoing analysis; recently, Tybur et al. (2020) failed to detect any effects of illness recency on attentional bias for disfigured faces, even though their sample size was four times that included in the original study by Miller and Maner (2011) study. As a final illustration of this type of relation, a greater sensitivity to negative experiences is observed when inflammation increases (Gassen & Hill, 2019). Thus, the study by Gassen and Hill shows that an inflammation caused by an endotoxin (versus a placebo) increases the activity of the amygdala in response to socially frightening photos (e.g., threatening faces) when compared with the perception of socially non-threatening photos (e.g., snakes) or that of neutral photos such as household objects. These results show that both systems are involved and, more particularly, that the biological immune system can directly affect the behavioral immune system.

It has also been possible to observe relations acting in the opposite direction. In one experiment, participants saw photos associated either with illness (e.g., running nose, spots, skin wounds), or with physical threats such as armed persons brandishing their weapons. A blood sample was taken from the participants before and after seeing the pictures in question. The level of the cytokine interleukin-6[3] was measured. The production of these molecules was found to be higher after seeing the pathogen-related pictures than the pictures depicting "physical" threats. A "psychological" stimulus activated elements of the biological immune system, which produced inflammatory responses as if an agent had penetrated the body (Schaller, Miller, Gervais, Yager, & Chen, 2010). Finally, a last example relates to a natural physical barrier: the skin. When confronted with parasites, the skin secretes antibodies by producing epidermal and dermal cells. It is therefore an essential component of the biological immune system and possesses tactile sensitivity (Madison, 2003). The presence of disgust-inducing elements in the environment increases subjective intentions to scratch one's own skin and wash one's hands (Prokop, Fančovičová, & Fedor, 2014) and also increases skin sensitivity (Hunt, Cannell, Davenhill, Horsford, Fleischman, & Park, 2017). To demonstrate

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[3] When the white blood cells detect aforeign body such as a bacterium, they secrete messenger cells known as interleukin-6 cytokines, which are responsible for the inflammatory responses that are intended to cleanse the body from intrusions.

this, participants were placed for 60 seconds in front of a small container of maggots or, in the control condition, a small container of rice. The participants' skin sensitivity increased when they saw the maggots but not the container of rice, thus underscoring the integration of the defenses inherited during evolution when confronted with a risk of contamination.

CONCLUSION

As illustrated throughout this chapter, the prevalence of germs and the pressure which they have exerted on organisms have shaped many of our current (individual and collective) behaviors. For example, thanks to studies of the BIS, it is possible to better understand (but in no way justify!) the unease that many people may feel when confronted with an obese or disfigured person. The BIS is therefore one of our adaptations in the same way as the (better known) biological immune system.

We wish to end this chapter by touching on one particular aspect of the BIS: the *inclusive* behavioral immune system (Shakhar, 2019). Evolution has selected individuals who are capable of detecting (though not always reliably) the signs of illness in order to protect themselves. Nature has also undoubtedly selected the individuals who are best able to use various behaviors to demonstrate to those around them that they are ill. This is the case, for example, of behaviors such as withdrawal from society during convalescence or the fact of being less able to look after one's loved ones. Showing signs of illness to others permits social immunity, or in other words collective protection such as the use of quarantine during epidemics. This makes it possible to "neutralize" the risk of pathogens, or at least slow down their propagation. With regard to quarantine in particular, one historical event is enlightening. In 1665 in England, when the plague was ravaging London, cloth from the capital containing fleas that were carrying the virus arrived in the small village of Eyam. The tailor was thus the first victim. The priest succeeded in convincing the inhabitants to stay indoors and place the village under quarantine, in this way forming a *cordon sanitaire*. As a result, no-one was able to enter or leave the village, thus preventing the neighboring villages—which contributed to the collective effort by bringing provisions and other items necessary for survival—from suffering the same fate. Claiming its last victim on November 1st, 1666, the epidemic came to an end after being responsible for 260 deaths, or approximately three quarters of the village. Without this great sacrifice, the overall death toll would have been much higher if the epidemic had spread to the neighboring villages. This type of collective behavior—painful though it may be because it runs counter to our hypersociality (DeWaal, 2010)—shows that the BIS is also inclusive. To conclude, in the spring of 2020 at the time when we are writing this chapter, a large part of the world's population is in lockdown: approximately three billion humans around the globe have had their freedom of movement restricted (Simpson & Katsanis, 2020) in an attempt to slow the spread of the coronavirus SARS-CoV-2. This moment of loss of freedom sadly reminds us that pathogens have always been a threat to human beings because they are the companions of our evolutionary history. These "invisible beings" have shaped our psychology and will continue to do so for as long as human beings populate the Earth.

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