



Review

Threat detection: Behavioral practices in animals and humans

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ABSTRACT

In contrast to a perceptible threat that releases freezing, fleeing and fighting, abstract potential threat elicits anxiety and vigilance. The prevalent view is that the larger the animal groups the lower the individual vigilance. Vigilance is a reflection of anxiety, and here we show that anxiety is contagious in grouped social animals. In humans, anxiety frequently results in rituals that confer a sense of controllability and thereby a means to cope with anxiety. Accordingly, in mental disorders with sustained anxiety, rituals predominate the behavior and consequently reduce functionality. Finally, the adaptive value of precautionary behavior, including rituals, lies in providing individuals with the opportunity to practice defensive means safely, and thus to prepare for the eventuality of real danger. Accordingly, the prevalence of anxiety in human and animal behavior accords with the “better safe than sorry” principle.

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1. Prolog

Both humans and other animals display emotions of fear and anxiety. While fear is the response to a perceptible threat such as fire or an attacking predator, anxiety is the response to an abstract danger, such as the potential risk of severe earthquake, or smelling the olfactory signals of a predator, signals that may attest its possible presence in the vicinity (Ohman, 2000). Ever since the seminal study of Darwin (Darwin, 1872), fear and anxiety have been considered as homologous in animals and humans (see Dalgleish, 2004 for a review on the history of the research on emotions). Implicit in Darwin's notion was the idea that fear and anxiety are essential for

survival since they trigger vestigial defense responses. In the face of perceptible threat, the defensive behavioral response is generalized into three forms: freezing, fleeing or fighting (Eilam, 2005). Freezing is exercised in order to fade from the enemy's attention; fleeing is aimed at increasing the distance from the danger; while fighting back is intended to dissuade the enemy (Blanchard, 1997; Blanchard et al., 1991; Blanchard and Blanchard, 1989). In each case, an obvious end to the conflict occurs when the opponents can no longer detect one another. From that point onward, post-traumatic anxiety may arise but not fear, since the danger is now obscure. Anxiety, however, is not always or necessarily post-traumatic since humans and animals may perceive a certain situation as risky, and consequently display risk assessment in order to avoid the danger or be prepared in advance for a potentially negative event (Barlow, 2000; Herwig et al., 2007; Blanchard et al., 2011). It is noteworthy that, unlike fear, in anxiety there is no external termination signal that may alleviate it. In other words, an animal that is anxious about the possibility of a nearby predator, might then come face to face with a predator, which will convert the anxiety into a real and

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perceptible danger that produces a fear response. Alternatively, the anxious animal might not encounter a predator, and the question is then one of when it will calm down and become less anxious. Relief from a state of anxiety is subjective and thus varies among individuals. It is based on the individual's risk assessment, which involves gathering information regarding the threat in order to produce an optimal response (Blanchard et al., 1991, 2011). Both fear and anxiety can be experienced by individuals or by large communities. For example, seeing a snake or being concerned with contamination or contracting a serious illness may be a threat to individuals, whereas war, terror, earthquake, or a tsunami may simultaneously affect entire nations or communities (Lowe and Fothergill, 2003; Tierney et al., 2001). This raises the question of the social impact of an anxious society on individuals; or, in other words, what is the difference between being exposed to a threat individually or as a group? Finally, while the aforementioned threats are external, other threats may stem from internal reasons such as conflicting motives and desires in normal behavior, or obsessive illusionary images of death and horrific events in anxiety disorders. In this survey, we discuss precautionary behavior in animals and humans under either real, abstract or illusionary threat. We mainly focus on two themes: (i) precautionary behavior in groups or solitary individuals (humans or animals) that have experienced a real life-threat and (ii) behavior in a pathologic state of sustained anxiety in obsessive-compulsive behavior. In both cases, precautionary behavior is manifested in excess due to a salient evolutionary shaping force: the real life-threat of predation in the former situation or a strong biological–psychological impact of sustained illusionary threat in the latter pathological situation. Common to both situations is the uncontrollability and unpredictability of the threat, and we therefore suggest that a salient characteristic of precaution in humans is that of ritual-like behavior, which is executed according to explicit rules and thereby confers a sense of controllability and predictability.

2. Behavior in the face of a real life-threat: an automated response but with a grain of discernment

“Some have been thought brave because they were too afraid to run away” (English proverb)

Upon encountering a perceptible life-threat, humans and animals need to respond appropriately, since a split-second decision can make a life or death difference. This split-second decision usually represents an adaptive defense response, which takes the form of freezing, fleeing or fighting back (Blanchard, 1997; Blanchard et al., 1991; Blanchard and Blanchard, 1989) – three basic and general defense responses that span the animal kingdom (Eilam, 2005). Before undertaking any of the three responses, however, some discernment is necessary and even within each response there is a certain hiatus for such consideration (Blanchard et al., 2011). An example of the flexibility obtaining within each defense is that of four different patterns of freezing that were revealed in the behavior of rats, with each pattern associated with a different contextual threat (Brandão et al., 2008). An additional example is that of vervet monkeys (*Cercopithecus aethiops*) that emit alarm calls that vary according to the presence of a terrestrial or an aerial predator (Seyfarth and Cheney, 1980, 1986). Domestic chickens (*Gallus gallus*) too produce alarm calls that may be differentiated along the same lines (Collias, 1987; Evans et al., 1993), and woodmice (*Apodemus mystacinus*) either freeze or leap when exposed to stoats (*Mustela ermina*) (Erlinge et al., 1974) but scamper away when exposed to other predators (Bolles, 1970; King, 1985). See Neuroscience and Biobehavioral Reviews, Vol. 21(6) for several reviews on the different perspectives of defensive behavior.

Making a judgment about the appropriate response before reacting is individual and subjective, giving rise to variation. Such variation has an important adaptive value in preventing the predator from predicting the defense response of the prey, despite the latter's limited defense repertoire. Accordingly, despite resorting only to freezing or fleeing responses, voles display a wide range of variety to owl attack within these responses: some freeze, others flee, while yet others switch several times or alternate frequently between freezing and fleeing (Edut and Eilam, 2004, 2003). These various combinations face the owl with a random rather than predictable response of an individual vole. Such random patterns have been termed ‘protean behavior’, named after Proteus, a sea god in Greek mythology, who could change his shape at will in order to confuse others. In the same vein, while individual cockroaches displayed some regularity in the direction of escape routes, the accumulation of the individual directions of a population of cockroaches adds up to a set of variable (random) escape routes. Accordingly, it was suggested that by utilizing multimodal escape options, cockroaches demonstrate an unpredictable defense response (Domenici et al., 2008). It should be noted that the above examples of voles and cockroaches illustrate that although the defense response of specific individuals is relatively fix, it varies among individuals and thus confronts the opponent with an unpredictable defense reaction. An unpredictable response also emerged within the same defense response of fleeing in spiny mice (*Acomys cahirinus*) when attacked by an owl. Some of these mice waited for the last moment in their attempt to escape whereas other fled as soon as they noticed the attacking owl (Ilany and Eilam, 2008). This behavior illustrates again the pre-response individual discernment, since implicit in executing a last moment escape is the ability to discern when is the last moment. Moreover, a decision to escape involves other judgments such as in which direction to escape: away from the predator in order to increase the distance from it, or toward it in order to kinematically impede its attack (Fishman, 1999; Hochachka, 2004; Shiffman and Eilam, 2004). Discerning the trajectory of escape is also important, with movement along a straight path being more efficient when escaping a slow or distant predator, whereas a zigzag path is advantageous when escaping a nearby or fast predator (Furuichi, 2002). Variation in precautions and risk avoidance were also correlate with age (Boyer and Bergstrom, 2011; Lienard, 2010). All in all, the above examples demonstrate that precaution behavior varies, and even the seemingly split-second response to a perceptible life-threat involves the discernment of various factors. This requires fast and flexible control mechanisms that able to adjust to the circumstances in order to provide an optimal defense response.

3. Anxiety and precaution: defense response without an identifiable triggering threat

“He who was bitten by a snake avoids tall grass” (a Chinese proverb)

So far we have discussed the response to perceptible life-threat. Humans and other animals, however, are also capable of risk assessment, followed by precautionary measures undertaken in order to avoid the potential danger (Blanchard et al., 2011). Risk assessment (Blanchard et al., 1991) involves gathering information regarding a potential threat in order to produce an optimal response. In animal behavior this is manifested as vigilance, which is alertness or readiness to detect events that could be of serious concern to the animal and its companions (Immelmann and Beer, 1989). A very familiar form of vigilance is that of a bird ceasing to peck for seeds or insects in order to scan the environment. It was demonstrated that this scanning is specifically aimed at detecting approaching predators (Bednekoff and Lima, 1998). Sequences of vigilance consist in

bouts of low-quality detection (active feeding) interspersed with bouts of higher-quality detection (overt vigilance) that can only be accomplished at the expense of feeding (Lima and Bednekoff, 1999).

Vigilant scanning was described in a wide range of animals (e.g. ostriches: Bertram, 1980; and antelopes: Underwood, 1982), with a reduction in individual vigilance occurring in parallel with an increase in group-size: the larger the group, the lower the level of individual vigilance and the greater the sum of collective vigilance (Bednekoff and Lima, 1998; Elgar, 1989). This makes it clearly advantageous to socialize in herds and flocks, thereby illustrating the impact of precaution as a ‘prime mover of social evolution’ (Wilson, 1975). Herds and flocks are able to be less vigilant than solitary conspecifics because grouping increases the collective likelihood of threat detection and thus reduces the likelihood that any given individual will be preyed upon (Dehn, 1990). Further analyses revealed that individuals at the perimeter of herds are more vigilant than those in the center (Elgar, 1989; Quenette, 1990) and, accordingly, herds of some species, like the African buffalo (*Syncerus caffer*), migrate in a column-shaped formation led by “pathfinders”, with the fierce adult males at the perimeter, and the females, calves and subordinate males in the center (Molszewski, 1983). This example of the buffalo demonstrates that, in populations, behavior under threat involves a socio-cultural component. This social component is notable in species that display communal vigilance, with a few individuals guarding the group while the others forage (meerkats: le Roux et al., 2009; hyraxes: Kotler et al., 1999; and babblers: Bergstrom and Lachmann, 2001). The precautionary behavior of the guards gives them in return a higher social status, and accordingly, better access to reproduction (Zahavi and Zahavi, 1997). All in all, the general notion in social animals is that higher vigilance by certain individuals enables other individuals to reduce their vigilance.

The above examples of vigilance in social animals, however, overlook another important, yet opposite, perspective of group vigilance: that anxiety, and thus also vigilance, are contagious. Indeed, being among a group of vigilant, watchful and worried conspecifics might exert a contagious effect and, in consequence, other individuals may also become vigilant, watchful and worried (Sirot and Touzalin, 2009). In a recent study we exposed voles to owl attack while the voles were in a group with their mates in their home cage. We placed this group of caged voles for overnight in an aviary in which barn owls (*Tyto alba*) could freely fly. The owls’ food (pieces of meat) was placed on the wire-mesh roof of the voles’ cage; thus the voles were exposed to real owl attacks, but the owls could not physically harm them. The anxiety level of each vole was assessed the night before and night after exposure to the owls, using two parameters: time spent by the vole in the open arms of an elevated plus-maze; and time spent away from the walls of an open field (Izhar and Eilam, 2010). Both the plus-maze and the open field are common apparatuses for assessing anxiety level. The elevated plus-maze is a cross of four similar horizontally-elevated arms, with two opposite arms being enclosed by side walls and the other two arms open as bare cliffs. A rodent is placed in the center of the plus-maze and the time it spends in the open or closed arms is measured under the assumption that the more anxious the animal, the less time it will spend in the open, less protected arms (Wall and Messier, 2001). Similarly, the open field is a walled empty arena. A rodent is introduced into the arena and the time it spends in the exposed arena center is measured compared with the time it spends near the arena walls. The more anxious the rodent, the less time it spends away from the arena walls (Prut and Belzung, 2003; Whishaw et al., 2006). Thus, in both apparatuses, the more anxious the animal, the less time it spends in the open sectors. In the present test, each vole was individually tested in these apparatuses 24 h before and 24 h after the group’s exposure to the owls. We found that the large individual differences in the voles’ anxiety measured before expo-

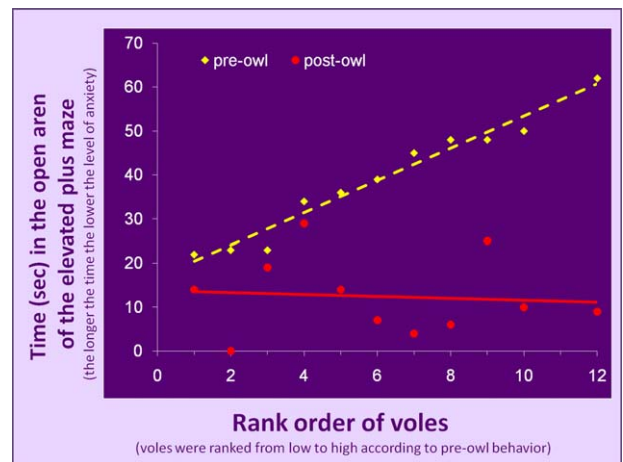


Fig. 1. Time spent in the open arms of the elevated plus-maze by 12 individual social voles that were housed together as a group. This measure represents anxiety: the longer the time spent, the less anxious the vole. Each individual vole was tested 24 h before and after an overnight in the owls’ aviary. In this figure, data of the voles’ pre-exposure to owls were depicted by yellow diamonds (◆), ranked along the x-axis from low to high according to the time spent in the open arms 24 h before exposure to the owls. That is, the more anxious voles are at the left and the less anxious at the right side of the scale of the x-axis. An inclined linear fit (yellow dashed line) represents the scattering of the voles along a wide range of anxiety level. Time in the open arms of the plus-maze 24 h after exposure to the owls is depicted for each vole by a red circle (●), with the datum of each vole paired with its pre-exposure datum. A horizontal linear fit of the post-exposure data (red solid line) indicates reduced time at the open arms and reduced variability compared with the pre-exposure variability.

sure to the owls were significantly reduced following exposure. In other words, after spending overnight in the owls’ aviary, the individual voles had all attained a similar level of anxiety, as measured in the elevated plus-maze and open field (Izhar and Eilam, 2010). A follow-up to this experiment is presented in Fig. 1, which illustrates that, normally, before any life-threatening procedure, social voles that lived in groups varied in their anxiety levels, as measured by the time they spent in the open arms of the elevated plus-maze. Accordingly, when these voles are ranked from low to high according to the time spent in the open arms before exposure to the owls, they fit an inclined line (yellow dashed line; Fig. 1). However, when the same individuals were tested 24 h after the life-threatening event (overnight in owls’ cage) they converged to a similar level of anxiety, fitting the horizontal line (solid red line; Fig. 1). Moreover, the low level of the horizontal line indicates that these voles hardly emerged from the closed arms of the elevated plus-maze, a behavior indicative of high anxiety.

In order to confirm that the convergence of anxiety at a similar level was a contagious group-effect, another group of voles underwent the same threatening night in the owls’ aviary, but this time they were caged individually throughout the test, isolated from their group mates. On the night before exposure to the owls, these isolated voles varied in their anxiety levels as measured by the time spent in the open arms of the plus-maze, and when ranked from low (more anxious) to high (less anxious), they fit an inclined line (yellow dashed line in Fig. 2). When the same isolated individuals were tested in the elevated plus-maze one night after the life-threatening event (overnight in owls’ cage) their anxiety increased (lower red solid line in Fig. 2 that represents less time spent in the open arms of the elevated plus-maze). However, the parallel orientation between the solid red- and yellow dashed-lines in Fig. 2 indicates that, on average, the effect of threat on the isolated individuals was similar, and the variability among them was preserved rather than diminishing as it had done in the grouped voles. Notably, min-max variability in the isolated voles was about 3-fold greater than in the grouped voles, and their anxiety, as measured by the time spent in

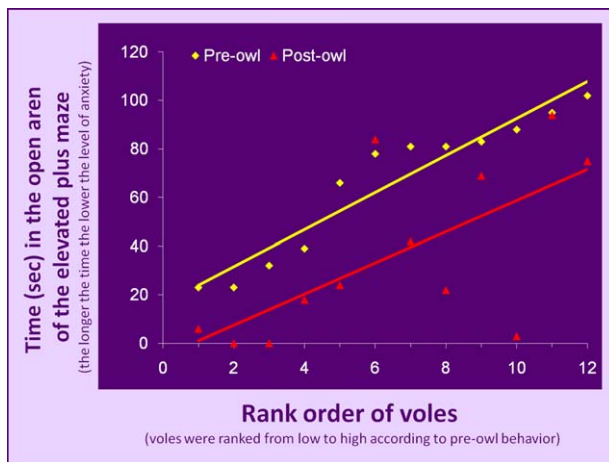


Fig. 2. Time spent in the open arms of the elevated plus-maze by 12 individual social voles that were housed isolated from each other. The layout of this figure is identical to that of Fig. 1. However, the pre-exposure (yellow dashed line) and post-exposure (red solid line) linear fit are parallel, indicating that the behavior of individuals was equally shifted by the threat, without the convergence to the same level that was apparent in the grouped voles shown in Fig. 1.

the open arms of the elevated plus-maze, was 3-fold lower (time in the open arms was 12.5 ± 2.8 and 36.4 ± 10.6 s in grouped vs. isolated voles, respectively; $t_{13} = 2.29$, $p = 0.039$; the longer the time at the open, the less anxious the animal). Nevertheless, the main group-effect was that of adopting the same “behavioral code” by different group members under stress. Indeed, some voles may display increased anxiety while others may temper down fearfulness, thereby reducing overall variability (Izhar and Eilam, 2010). Altogether, these data illustrate that, in social animals, precautionary behavior is socially facilitated. That is, groups under threat display reduced individual variation as if they have adopted a similar, common behavioral code (Izhar and Eilam, 2010).

The above convergence of behavior to a uniform level is reminiscent of a specific aspect of social human behavior following a disaster, when adopting a similar behavioral code is expressed as integrative responses of solidarity, altruism, loyalty and volunteering (Tierney et al., 2001), as for example emerged after the September 11th attack on the World Trade Center in New York (Lowe and Fothergill, 2003). Indeed, after this attack many individuals demonstrated increased prosocial behavior (Poulin et al., 2009). It was argued that Americans have become more committed to family, more spiritual, more public-minded, express greater interest in volunteering, show stronger feelings toward nation and community, and express higher levels of patriotism (Etzioni, 2002). Adoption of a strict behavioral code is also apparent on other occasions of stressful events, as for example among family members following bereavement (Lehman et al., 1993). Moreover, it was shown that the above types of social response similarly emerged following a disaster among a large spectrum of individuals differing in age, occupation, income, ethnic background, gender and sexual preferences (Lowe and Fothergill, 2003). Accordingly, the findings in voles (Izhar and Eilam, 2010, and Figs. 1 and 2) present a novel model for studying the impact of a life-threatening event on social groups. Nonetheless, the above less-noticed positive facets of horrific situations are generally outweighed by the undesired consequences, such as severe post-traumatic stress disorder (Bleich et al., 2003; Richman et al., 2009) and domestic violence (Wilson et al., 1998). Indeed, no-one would appear to anticipate a disaster for its benefits; rather, humans and animals tend to become anxious at the prospect of a potential threatening event.

The notion behind the above vole experiments was that, in social groups, anxiety and thereby vigilance is socially facilitated (Siro

and Touzalin, 2009). In other words, while on the one hand being among vigilant individuals enables foraging with peace of mind, such vigilance may also be contagious so that all individuals become vigilant, watchful and worried. Some biological support for this notion is implicit in a study that illustrates that, in humans, fear is contagious via the transmission of chemosignals of fearful sweat (Zhou and Chen, 2009).

Vigilance is also based on past experience, either inherited as an evolutionarily adaptive trait or on the basis of the individual's life history. Evolutionary theory predicts that we behave adaptively, which means that behavioral phenotypes converge (on average) towards an optimum. Accordingly, it was suggested that anxiety and the consequent precautionary behavior, and specifically risk assessment, are adaptive and vital since they enable an individual to practice defensive means in total physical safety, so that when the mishap of real threat occurs, that individual is already primed to take the appropriate defensive reaction (Abed and de Pauw, 1998–1999). By virtue of natural selection, such adaptive behavioral traits are then fed into the gene pool, resulting in precautionary behavior that is highly adapted to environmental threats. For example, in the desert, owls hunt in open spaces whereas snakes hunt among shrubs. Accordingly, it was found that on moonlit nights with high visibility and high risk of owl attack, wild rodents forage near shrubs and avoid open spaces, whereas on dark nights with low visibility and lower risk of owl attack they forage in the open and avoid shrubs where snakes hunt (Abramsky et al., 1996; Kotler et al., 1992). This last example of desert rodents illustrates the adaptive value of risk assessment and precautionary behavior, along with the embedded complexity of anxiety as an emotional state that does not require real external threat.

4. Bringing order into chaos: the emergence of motor rituals under anxiety

“This is the way you brush your hair, brush your hair, brush your hair” (Children's nursery rhyme)

Precautionary behaviors may not occur independently. As they emerge under regulatory mechanisms (functional, biological or cultural ‘constraint’), they may become integrated with other traits into a ‘ritual’. Indeed, anxious humans are often preoccupied with rituals and several studies have hypothesized that these rituals are the result of threat to fitness (Boyer and Lienard, 2006, 2008). Ritual performance is intended to reduce anxiety, and is characterized by vigor, precision and high concentration (Boyer and Lienard, 2006; Eilam et al., 2006). These characteristics are striking in intensive religious rituals that enhance concentration during rigorous prayer, or in sport rituals that are aimed at facilitating concentration on performance and disassociation from the spectators (Boyer and Lienard, 2006, 2008). The vigor, precision and high concentration in ritual performance reflect high controllability and make the behavior very predictable for the observer. We suggest that these facets of controllability and predictability constitute a counter-reaction of the individual to the anxiety that is the result of threats that are perceived to be uncontrollable or unavoidable (Ohman, 2000), as illustrated in the examples presented at the beginning of this survey: confronting a venomous snake, contamination or contracting a serious illness, war, terror, earthquake and tsunami. All these are events that we normally cannot control or predict and they therefore become anxiogenic. Since uncontrollability and unpredictability are major stressors (Foa et al., 1992), a repeated and precise performance of the same acts can generate a sense of controllability and a consequent reduction in fear from the abstract threat. This process is illustrated in the story of a child in the dark (Deleuze and Guattari, 1987); p. 311. The child, “gripped with fear, comforts himself by singing under his breath. . . lost, he takes shelter,

or orients himself with his little song. . . The song is like a . . . calm and stable center in the heart of chaos". This effect of the repeated song was further described as follows: "The song is calming, a stability amidst the chaos, the beginning of order. The song marks a space, the repetition of the simple phrases structures that space and creates a milieu. . . The song begins a home, the establishment of a space of comfort" (Wise, 2000). The same purpose of gaining controllability and reducing unpredictability applies to superstitious behavior (Lindeman and Saher, 2007; Rudski, 2003) in which people try to gain control over their fate, their future, random gambling games or events beyond their influence such as in sport. For example, a person may believe that through his precise performance of a certain ritual, his sports team will win the game. In performing this ritual, the person who was anxious about losing the game obtains the comforting (albeit false) feeling that he has some control over its outcome.

While repeated rituals present a salient hallmark that can emerge in humans due to inferred threats to their fitness (Boyer and Lienard, 2006), repeated stereotyped ritual-like activity was described in a large spectrum of domestic, farm and caged species (Cabib, 1993; Carlstead and Steidensticker, 1993; Fraser and Broom, 1990; Hediger, 1964; Meyer-Holzapfel, 1968; Stevenson, 1983). It was presumed that these stereotypies reflect the stress and frustration induced by the captive environment (Dantzer and Normede, 1983; Duncan and Wood-Gush, 1972; Keiper, 1970; Rushen, 1984). Four parallel processes were suggested to take place during the emergence of stereotyped motor rituals in animals: (a) increase in activity, (b) repetitive locomotion along the same few paths, (c) increase in the incidence of stopping in a few specific places, along with a decrease in stopping at other places and (d) emergence of relatively fixed motor rituals in stopping places (Ben-Pazi et al., 2001). Consequently, stereotyped behavior is regarded as a normal behavior that becomes overly repetitive along with losing flexibility (Mason, 1991; Mason and Turner, 1993). Like human rituals that result in reduced anxiety, cage stereotypies also reduce anxiety, although paradoxically they reflect the poor animal welfare that accounts for the emergence of stereotypy. Indeed, it was found that within similar captive environments, the levels of corticosteroids, which offer a good indication of stress, were lower in stereotyping compared with non-stereotyping individuals (Koolhaas et al., 1999; Redbo, 1993; Wexhsler, 1995). A certain relief of anxiety by virtue of ritual-like behavior was also reported in humans suffering from obsessive-compulsive disorder (OCD; see next section). Specifically, OCD patients reported that they gain relief from anxiety through the repetitive performance of rituals (Rapoport, 1989a,b, 1990). However, such an anxiolytic effect was usually gained only when an adequate sense of completion of the ritual had been achieved (Szechtman and Woody, 2004), while interruption or blocking of the ritualistic activity often aggravated the anxiety (Goodman et al., 1989). In the same vein, it was suggested that: "cultural rituals and OCD are characterized by a desire to produce order, regularity, boundaries and clearly demarcated categories" (Fiske and Haslam, 1997), p. 221. In all, therefore, behavior under anxiety and apprehension, as in the story of the child in the dark (Deleuze and Guattari, 1987), usually takes the form of repetitive, ritual-like behavior, with the repetitive behavior being beneficial in reducing anxiety and bringing order into chaos.

5. Sustained sense of illusory threat: a pathology that turns order into chaos

"He who fears to suffer, suffers from fear" (English proverb)

Many psychiatric disorders reflect various evolutionary perspectives of self-defense, an exaggerated or persistent form of normal defensive reactions (Beck, 1996). Psychiatric syndromes are

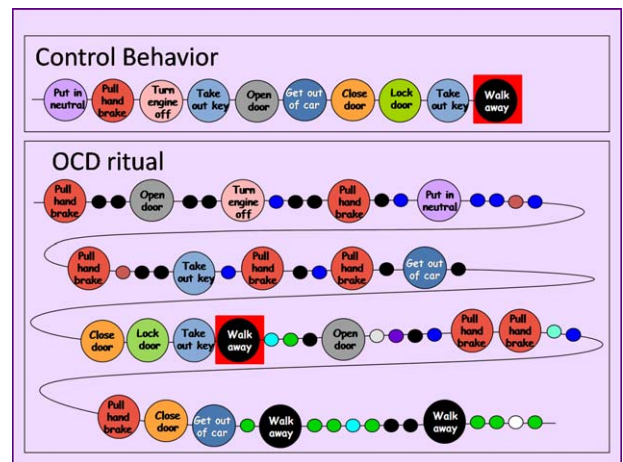


Fig. 3. The sequential order of shared/functional (large circles) and unique/non-functional (small circles) acts in a ritual of 'locking the car' as performed by an OCD patient (bottom) and the matched non-OCD control (top). Shared acts (large circles) are also matched in color between the OCD and non-OCD sequences. As shown, the control individual performed a sequence of consecutive shared acts (large circles) with no unique acts. In contrast, for the OCD patient the sequence of shared acts (large circles) is interrupted by numerous unique acts.

heavily affected by a lower sensitivity threshold to threats, which in turn results in excessive activation of risk assessment systems (Flannelly et al., 2007). In this context, obsessive-compulsive disorder (OCD) is a common anxiety disorder in which many patients are preoccupied with activities that are supposed to diminish their illusory fear of potential danger from contamination, contagion, risk to kin, etc. Notably, OCD is a severe chronic psychiatric problem with a prevalence rate of 1–3%, listed by the World Health Organization among the ten most debilitating illnesses in existence (El-Sayegh et al., 2003). It was suggested that the underlying mechanism in OCD is hyperactivity of a security motivation system (Szechtman and Woody, 2004) or of a precautionary system (Boyer and Lienard, 2006). Accordingly, the anxious patient performs a ritual in order to allay the fear of an illusory unreal threat, but since there is no feedback signal or a 'sense of knowing' that the precautionary task has been completed, the ritual is repeated time and again (Szechtman and Woody, 2004). OCD patients are preoccupied in ritualization, and their behavior becomes an endless set of rituals that neutralize normal functioning. The question thus arises as to what in rituals interferes with normal functioning.

To answer this question, rituals of OCD patients were each compared with the behavior of a respective non-OCD individual who was instructed to perform the same task that the OCD patient ascribed to the ritual. This methodology established a data set of pairs of rituals, with each pair comprising an OCD and a non-OCD performance of the same task. The acts performed by each such pair were divided into two categories: acts that were shared by both the OCD patient and his/her respective control, and the acts that were performed by only the patient but not by the control (small circles), whereas acts shared by both the control and the OCD patient (large circles) were frequently repeated by the OCD patient, but not by the control person. This illustrates two conspicuous features of OCD rituals: repetition of acts and addition

of numerous superfluous acts (Zor et al., 2009a). The acts performed by both the control individual and the OCD patient (large circles) may be considered as “functional”, whereas the acts “unique” to each individual may be considered as “non-functional” since, as illustrated in the example shown in Fig. 3, each individual accomplished the task without performing the “unique” acts of the other person. The pathology of OCD behavior then becomes obvious: the unique acts (small circles) break down the “functional” sequence of acts into a few elements, compared with the long sequence of functional acts in the control (Fig. 3). That is, functional performance in OCD is interrupted by numerous unnecessary non-functional acts. By applying this analytic methodology to rituals of a group of OCD patient, it was argued that the abundance of unique irrelevant or unnecessary acts in OCD represents reduced functionality in terms of task completion and, in consequence, at least some aspects of OCD may indicate a disorder of repetitive and pessimal behavior (antonym of optimal behavior; Zor et al., 2009b). Altogether, it is a sad aspect of OCD that the quest of the patients for order, as reflected in their ordering, cleaning, aligning and checking activities, results in a severe and debilitating mental disorder (Zor et al., 2009b).

Motor rituals also occur in patients with psychiatric disorders other than OCD (Fineberg et al., 2007; Hollander, 1993; Hollander et al., 2005), as well as in normal individuals (e.g., the aforementioned sport and religious rituals). It would seem that rituals with the same themes of OCD behavior also occur in cultural rituals and in the routines of many children (Boyer and Lienard, 2006; Jencius and Rotter, 1998), and these rituals in normal behavior seem remarkably similar to the compulsions of OCD patients (e.g. Dulaney and Fiske, 1994; Fiske and Haslam, 1997; Pallanti, 2008; Turbott, 1997). While it was assumed that OCD rituals may comprise a cultural component, the findings of comparative studies suggest that obsessive-compulsive disorder is more deeply embedded in common neurobiology than in cultural differences (Pallanti, 2008; Zor et al., 2010). Since behavior is the ultimate output of the nervous system, the similarity between OCD and normal behavior probably reflects a parallel similarity in the controlling neural mechanisms of these behaviors. Hypotheses on the underlying mechanism of rituals, such as the security motivation system (Szechtman and Woody, 2004), harm avoidance (Ecker and Gönner, 2008), threat to fitness and precautionary system (Boyer and Lienard, 2006) or psychological immune system (Abed and de Pauw, 1998–1999), lead us to the next section, on the possible controlling mechanisms of precautionary behavior.

6. Epilogue

“Better safe than sorry” (English proverb)

Threat generates profound changes in behavior via its controlling mechanisms. Individuals (humans or animals) may respond to overt threat to life by freezing or fleeing (Blanchard, 1997; Eilam, 2005), whereas populations may include a socio-cultural component in threat response. In animals, life-threatening events generate profound changes in behavior (Eilam et al., 1999), in its controlling mechanisms (Canteras, 2002), in vital activities such as foraging (Kotler et al., 1992; Kotler et al., 1994) and reproduction (Vasilieva et al., 2000), in local population changes (Berger, 1991; Wooster and Sih, 1995), and ultimately in ecosystems, due to a shift in the balance between prey and predator populations (Abrams, 1995; Turner, 1997). The primer in this cascade of changes is the individual response to danger.

Human, and perhaps also non-human brains, have threat detection systems that are dedicated to inducing the following three phases: (i) identifying particular cues of potential danger; (ii) activating appropriate precautions and (iii) after precautions are taken,

providing a sense of safety. The first phase is probably the one which is most understood (Lang et al., 2000; Ninan, 1999). Sensory information, for example the sight, sound or odor of a predator, triggers the senses. In the second phase, information on the threat is delivered to the amygdala, which generates an immediate response (freezing, fleeing, defensive fight) and then via the hypothalamus which boosts stress-hormone release, races the heartbeat and shuts off the digestive system. In parallel, information is transferred to the cortex for further consideration of the necessary response (risk assessment) based on experience and innate defensive behavioral templates, and some cognitive consideration (at least in humans) of the situation (Flannelly et al., 2007). However, the third phase, that of suppressing the response to stress, has remained elusive. Anxiety by its nature is a paramount response to an abstract potential threat, and, as mentioned above, there is no external signal that might stop it. Rather, as described above, the stop signal is subjective and internal, being based on consideration of the situation on the basis of past experience. This subjective stop point is a sort of “feeling of knowing” that signals task completion and terminates the activated defense response. To distinguish between the general use of the term “feeling of knowing” and its applicability to precautionary behavior, the term *yedassentience* was proposed to signify the stop signal for the activation of the security motivation system (Szechtman and Woody, 2004; Woody and Szechtman, 2010); the term was derived from the Hebrew *yeda* [knowing] and the Latin *sentire* [to feel]. In the same vein, it was suggested that obsessions consist in a train of unproductive and prolonged intrusive thoughts or ideas that are ruminated without “a fixed end-point at which the person feels some satisfaction or relief and so can stop” (de-Silva, 2003), p. 198. Taking together the aforementioned notions, it was suggested that risk assessment and the consequent defense response are controlled at three hierarchal brain levels: (i) the basal ganglia; (ii) the limbic system and (iii) the prefrontal cortex (Flannelly et al., 2007). According to this model of hierarchal levels, the first two levels evolved before consciousness and therefore account for these levels representing pre-conscious and pre-emotional levels (Tsuchiya and Adolphs, 2007), whereas the prefrontal cortex is the highest and conscious level of processing stimuli related to fear, threat or danger and integrating cognitive information such as experience and beliefs with information from subcortical structures (Davis, 1998; Flannelly et al., 2007; Mobbs et al., 2009; Morris et al., 1999) see LeDoux (2000) for review on brain circuits that control emotions and Woody and Szechtman (2010) for a model of the brain circuit of the security motivation system.

Anxiety, risk assessment, and the security motivation or precautionary systems, are adaptive and vital mechanisms that train and prepare individuals to confront stressful situations (Blanchard et al., 2011). These systems are biased towards perceiving threats even when they do not exist, under the principle that “it is better to be safe than sorry” (Gilbert, 1993, 2002). The adaptive value in this principle is that while individuals will know how to handle good and desired events and no adaptive means are required for this, they should be well prepared for any bad, threatening events (Herwig et al., 2007). That is, it is best not to take risks, even if risk avoidance requires time-consuming, boring and non-functional activities (e.g. rituals). Accordingly, precautionary systems tend to evaluate ambiguous situations as being dangerous rather than being safe (Baumeister et al., 2001; Leahy, 2002). After all, being careful is on the whole less likely to lead to a bad outcome.

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