The biological origins of rituals: An interdisciplinary perspective

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ARTICLE INFO

ABSTRACT

Ritual behavior is ubiquitous, marking animal motor patterns, normal and psychopathological behavior in human individuals as well as every human culture. Moreover, formal features of rituals appear to be highly conserved along phylogeny and characterized by a circular and spatio-temporal structure typical of habitual behavior with internal repetition of non-functional acts and redirection of attention to the "script" of the performance. A continuity, based on highly conserved cortico-striatal loops, can be traced from animal rituals to human individual and collective rituals with psychopathological compulsions at the crossing point. The transition from "routinization" to "ritualization" may have been promoted to deal with environmental unpredictability in non-social contexts and, through motor synchronization, to enhance intra-group cohesion and communication in social contexts.

Ultimately, ritual, following its biological constraints exerts a "homeostatic" function on the environment (social and non-social) under conditions of unpredictability.

1. Introduction

This contribution attempts to present an explanatory framework of rituals through an inter- disciplinary approach, linking ethology, psychopathology and anthropological sciences.

The search for a phenomenological continuity of rituals across different disciplines lies on three basic assumptions. First, rituals are ubiquitous, being found in animal behavioral patterns, as well as in humans in everyday routines, in specific stages of the life-cycle (especially childhood, pregnancy or motherhood) and in psychopathological conditions (i.e. Obsessive-Compulsive Disorder -OCD). Besides, ritualistic collective behaviors mark every human culture (Boyer and Lyenard, 2006).

Second, rituals appears to be constantly fixed into some invariant and specific formal characteristics, i.e. the internal repetition, the rigidity of the performance and the detachment from a goal-directed behavior (Keren et al., 2010). Of course, an increasing amount of complexity may be traced along phylogeny: from a purely automatic and stereotyped motor behavior at the one end to the integration of affective and cognitive processes that finally become deeply embedded within cultural symbolic meanings at the other end (Turbott, 1997).

Third, literature from both animal models of compulsive-like behavior and compulsions in different psychiatric conditions converge on

the critical role for the basal ganglia, a highly evolutionary conserved neural system implicated in complex and functionally distinct large-scale brain networks (Wilkes and Lewis, 2018).

The term "ritual" has been adopted to describe different forms of repetitive behavior such as stereotypies, fixed-action patterns and habitual behavior, so that a distinction of rituals from other forms of repetitive behavior is often not clear. Moreover, an interdisciplinary study of rituals is lacking (Dulaney and Fiske, 1994; Turbott, 1997; Boyer and Lyenard, 2006), affecting the possibility to capture the specificity of ritual phenomenon along a phylogenetic continuum.

Therefore, the present study aims at investigating if different forms of rituals, from invertebrates and vertebrates repetitive motor patterns to complex cultural manifestations, through human every-day individual physiological or pathological rituals, lie on a continuum, and, if so, to grasp the" ultimate causations" of such apparent highly conservative behavior.

The hypothesis of the present study is that rituals may have emerged as a co-option of pre-existing behavioral traits (i.e. an "exaptation" phenomenon): specifically, as a functional shift from habitual behavior in order to increase environmental (both social and non-social) stability under conditions of unpredictability. The epistemic background lies on the premise that human vulnerability to diseases is rooted in phylogenetic constraints and that our behavior and mind are shaped by

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evolutionary mechanisms deeply intertwined with brain developmental plasticity and culture (Palanza and Parmigiani, 2016).

2. Ethology of rituals

2.1. Fixed-action patterns

From an ethological perspective, rituals are described in terms of repetition and stereotypy (Payne, 1998). In classic ethology, the term "fixed-action pattern" (FAP) refers to species-specific, stereotyped sequence of behavior which was held to be innate (genetically pre-programmed) and relatively uninfluenced by learning (Immelmann and Beer, 1989). FAPs have also been found in human infant (Eibl-Eibesfeldt, 1989). Tinbergen (1953) demonstrated that FAPs are triggered by "specific external sign stimuli" (e.g. the red or swollen belly of a live conspecific or even a rough model triggering the attack or courtship FAPs respectively). Once the FAP is activated, the specific behavior pattern is fully expressed (Alcock, 1993). Actually, even in a highly stereotyped form, there is also a certain variability with behavioral patterns showing both fixed and variable components. Accordingly, the alternative term of "modal action pattern" (MAP) was proposed (Barrows, 1995). This inbuilt flexibility may be observed across the full phylogenetic spectrum. Also in invertebrates, innate behavior, far from being rigid and stereotyped, may be shaped according to environmental cues, metabolic demands and physiological states (Brembs, 2013). The high experience-dependent plasticity of behavior would be mediated by conserved signaling mechanisms (the cAMP/PKA/CREB pathways, underlying the formation of long-term memory (LTM) and associative learning) from mollusk to mammals (Cammarota et al., 2000). Besides, decision-making circuits responsible for activating innate social behaviors share common neural substrates in both Drosophila melanogaster and mice (Gelperin, 2017).

2.2. Habitual behavior

Habitual performance is highly stereotyped behavior that can be explained by its purpose (Eilam, 2015). Habitual behavior is normally placed into a fixed spatio-temporal structure (Eilam et al., 2006), that permits to order and schematize animal territory into a discrete set of places, each with a specific set of acts (Eilam et al., 2006). These places are then interconnected by fixed and regular routes (Hediger, 1964). The tendency to reorganize the territory into rigid spatio-temporal parameters has been observed both in vertebrates and invertebrates. It has been suggested that such behavioral rigidity has an adaptive value, allowing faster performances and less attention (Eilam et al., 2006). Moreover, simplifying a behavioral pattern via stereotypy, repetition and routinization permits to focus attention to threating external stimuli (Fentress, 1976). Of course, also routine motor displays show a certain degree of flexibility within and across individuals. Behavioral flexibility and variability (and its potential adaptive value) are guaranteed by irrelevant or unnecessary acts that are embedded within the motor pattern (Eilam, 2015). From an evolutionary perspective, behavioral variability would be an essential component in the evolution of behavioral patterns (like genetic variability in biology). In such a case, unnecessary acts would serve to retain a certain flexibility by irregularly interrupting the automatic performance, and thereby enabling the performer to maintain the awareness and control that are necessary for behavioral adjustment to changing circumstances (Keren et al., 2013). In other words, unnecessary or idiosyncratic acts prevent automated processing with no or minimal attention (Moors and De Houwer, 2006). In so doing, the motor sequence may be modifiable to fit the situation (Dumais, 1981) and to enable the organism to test its environment (Brembs, 2011).

Even though the highly rigid behaviors of FAPs and habitual behavior may be phenotypically undistinguishable, they differ in that FAPs are genetically pre-programmed whereas habitual behavior is the result of a learning process. Both of them imply predictability of the environmental context (social or non-social). FAPs represent phylogenetically programmed behavioral responses mediated by brain innate releasing mechanisms (Immelmann and Beer, 1989). Natural selection (via non-social environmental selective pressures) and sexual selection (via social environmental selective pressures) have genetically "fixed" the highly predictable relationship between the external stimulus and response. Conversely, in habitual behavior, the predictability of behavioral outcomes in a given environmental context is learned. Once learned, this behavior becomes automatic and highly functional without any further cognitive attention (Thorpe, 1958). Of course, this does not mean that an actual dichotomy exists between innate behavior and learning. Rather, behavior varies continuously from being almost entirely independent from learning to being highly dependent on learning. For example, "innate" behaviors may be preceded evolutionarily by learned forms of behavior, which are subsequently fixed into "canalized" behaviors (Tierney, 1986). The "continuity" between innate and learning behavior has been demonstrated both in invertebrates and vertebrates; in Aplysia for example, an automatic and rhythmic behavior can arise from a learning-induced "rigidification" of the functional properties of decision-making circuitries (Nargeot and Simmers, 2012).

Altogether, habitual behaviors are characterized by the following specific features: 1) they are largely learned (i.e. acquired via experience-dependent plasticity); 2) they occur repeatedly over the course of days or years and they can become remarkably "fixed"; 3) once acquired, habitual motor task is performed automatically, allowing attention to be focused elsewhere; 4) they tend to present a structured action sequence elicited by a particular context or stimulus (Graybiel, 2008).

Stereotypies are qualitatively distinguished from habitual behavior based on their apparent purposelessness and great repetitiveness. Whereas FAPs and habitual behavior are triggered in the course of normal behavior, stereotypies are most prominent under aversive conditions (such as stress, social isolation or sensory deprivation) (Ridley, 1994).

2.3. Rituals

Rituals are common across animal species. These behaviors share cardinal characteristics with habitual behavior: they are repetitive, sequential action streams and they can be triggered by particular cues (Graybiel, 2008). Indeed, routinized/habitual behavior appears to constitute the building blocks of rituals (Eilam, 2015). The transition from "routinization" to ritualization would be marked by an inflated performance of voluntary (i.e. non-automatic), unnecessary, non-functional acts (in addition to the functional ones) with the result to affect the pragmatic functionality of the basic motor pattern (Zor et al., 2009). The non-pragmatic redundancy of non-functional acts implies the loss of the automatic execution of the act with hyper-attention to the formal structure of the behavioral pattern (Krátký et al., 2016). Namely, the emphasis on fidelity and invariance of the performance, the rigid adherence to the "rules" (i.e. the precise execution of the "script") become the focus of cognitive efforts (Boyer and Lyenard, 2006) and the ultimate goal of the performance itself (regardless to its pragmatic function). Consistently, rituals would differ from habitual behavior for their "thoughtfulness" (Eilam et al., 2006); that is, whereas habitual behavior is performed automatically, rituals involve a shift of attentional focus to the basic structural units (acts) of the motor performance (the "script") (Zor et al., 2009).

2.3.1. Environmental predictability

It has been speculated that the redundancy of non-functional acts serves as a means to reduce anxiety and to gain a feeling of controllability and predictability (Eilam et al., 2011). Since early ethological observations (Lorenz, 1966), rituals have been described to be triggered

whenever the uncontrollability and unpredictability of the context increase, for example when habitual routines are abruptly interrupted or usual paths are changed. In this perspective, Lorenz (1966) has conceived animal rituals as a "proto-religious" behavior. Interestingly, also in invertebrates (e.g. Drosophila) the automaticity of the performance is related to the levels of environmental predictability, i.e. with a shift from automated habitual behavior to decision-making behavior when uncertainty increases (Schleyer et al., 2013). The interruption of an automatic/habitual performance for adjustment to changing circumstances has been also demonstrated in other insects. Particularly, wasps and bees perform a series of learning flights (re-orientation flights) to re-establish a visual representation of the nest environment when natural environment is no more predictable (e.g. when their nest has been displaced or if they had encountered difficulties in finding the nest on their preceding return) (Stürzl et al., 2016).

The repetition of non-functional acts (i.e. ritualization) would enhance behavioral plasticity (Eilam, 2015), necessary to face environmental unpredictability. In this regard, rituals would have evolved as a "homeostatic" behavior, aimed to acquire information and to cope with the new environment, and thereby re-establishing controllability and predictability (Blanchard et al., 1991). Therefore, the phylogeny of ritual is related to unpredictability-related anxiety (Lang et al., 2015; Krátký et al., 2016). Any time that the predictability of the environment is broken, rituals work to "re-establish" the pre-existing order with an anxiolytic effect. This is in line with the hypothesis of rituals as a security motivation system, evolved to handle the uncertainties of potential "disordering" threats (Szechtman and Woody, 2004; Woody and Szechtman, 2013).

2.3.2. Intra-specific communication and group cohesion

The second well-documented force to ritualization in animal kingdom is intra-specific communication. In this respect, FAPs are removed from their original context and incorporated into a signalling function (Immelmann and Beer, 1989). Through exaggeration and repetition, behavior gets divorced from its original pragmatic goal and "exapted" for a communicative value (i.e. ritualization phenomenon). For example, in gallinaceous birds, the evolution of the so-called pecking courtship behavior appears to be an exaptation of feeding behavior, in that the female was originally attracted by the possible presence of food (Stokes and Warrington Williams, 1971; Immelmann and Beer, 1989). The redundancy and exaggeration of the movement of pecking (i.e. its ritualization) might have evolved through female choice (intersexual selection) of males with an innate higher tendency to repetition and magnification of the act of pecking. Ritual development occurs through "an increase of conspicuousness by simplification and exaggeration of form, embellishment, repetition (usually rhythmical), emphasis of particular components, slowing down or speeding up of performance, addition of morphological support such as coloration and stereotypy" (Immelmann and Beer, 1989). In courtship behavior, ritualized communication is of utmost importance to species recognition. For example, ritualization of FAPs is invariably found in display behaviors linked to reproductive fitness. Sexual or social selection plays an important role in the evolution of intraspecific (intrasexual and/or intersexual) ritualized FAPs into courtship behaviors. In animals that mostly use vision in intraspecific communication, FAP effects are magnified by the evolution of particular body structures and/or colors (e.g. the peacock' tail, the red deer antlers etc.) displayed during the ritual performance. In this respect, behavioral plasticity (communication) can precede and instigate morphological evolution (Mayr, 1963; Palanza and Parmigiani, 2016; Allf et al., 2016).

Moreover, rituals promote behavioral synchronization that is the basis of intra-specific connection and communicative bonding (for example between sexual partners or in aggressive displays for competition over mates and resources). Patterns of synchronous activity have been found in almost every animal group studied, from multicellulars animals (Placozoa) to humans. Rather, synchrony plays a role in almost

every aspect of group behavior; synchronized activity promotes information processing within the group and allows to respond quickly and effectively to changing environmental conditions (such as the appearance of a predator), at the same time preserving the cohesion and organization of the group (Couzin, 2018). Group living organisms must synchronize their decision to find food or appropriate habitats or to avoid threats. Activity synchronization in colonies of cavity-dwelling ants or of giant honeybee are well documented (Cole, 1991; Kastberger et al., 2008), as well as synchronized behavior in animal collectives such as birds and fish. Interestingly, studies of the propagation of behavior and group cohesion in fish, birds and humans have shown a fundamental commonality in the mechanisms by which behavior spreads. For example, reinforcement tends to depend on the fraction of perceived individuals exhibiting a certain behavior rather than on the absolute number of other individuals (Rosenthal et al., 2015). Moreover, there in evidence from both fish and human studies that the propagation of behavior also depends on the structure of social networks (Ugander et al., 2012; Strandburg-Peshkin et al., 2013). Nevertheless, the mechanisms underlying the remarkable speed at which information propagates in some animal groups (e.g. starlings and silverside fish) is not completely understood. A hypothesis is that individuals are able to interact with a projected future state of the system (future position or velocities of other individuals) rather than the current state (Noy et al., 2011).

Altogether, rituals may have emerged from habitual behavior to enhance behavioral flexibility in order to face environmental unpredictability as well as to promote intra-group communication and cohesion.

3. Anthropology of rituals

Cultural anthropologists accept the definition of scripted, stereotypic forms of collective actions (Gluckman, 1975). Rituals are a constant tendency of every culture (Turner, 1985), remarkably persistent through history of mankind (Staal, 1989) and deeply connected with the experience of the Sacred (Penner, 1992).

Cultural rituals share common ideational and formal structures (Dulaney and Fiske, 1994). Exactly like in animal rituals, cultural rituals involve precise spatiotemporal arrays. Rather, collective rituals often serve for rigidly demarcate sacred and profane time and space (Eliade, 1959). Moreover, they share similar formal features: internal repetition and redundancy, "scriptedness", detachment from a pragmatic goal (Lienard and Lawson, 2008). Noteworthy, even when rituals are justified by mythological "explanations", they are inherently compelling, i.e. with a compulsory character (Rappaport, 1979; Tambiah, 1985; Dulaney and Fiske, 1994; Boyer and Lyenard, 2006). Of course, cultural rituals involve much more elements than a simple routinized motor behavior, often appearing as a multi-sensorial manifestation including costumes, masks, effigies, dances, as well as prayers, invocations, etc. Nonetheless, exactly like animal ritual behavior, cultural rituals are built on ordinary or habitual action sequences, performed in exaggerated and repeated forms and divorced from their original pragmatic function (such as ritual eating or drinking and so on) (Boyer and Lyenard, 2006). During ritual performance, ordinary actions are adopted in different contexts and often connected to non-ordinary or supernatural agents (Lawson and McCauley, 1990). Nevertheless, the parallel between human culturally evolved and biologically evolved animal rituals is relevant in that exaggerated habitual behaviors (in form, colors and so on) appear to be the building blocks of both forms of ritualization. Moreover, anthropological studies seem to converge on the same causations described for animal rituals, i.e. predictability of the environment and intra-specific communication.

3.1. Environmental predictability

The aim of increasing environmental predictability would be

implicit in ritual's etymon itself. Indeed, the etymology of ritual would derive from the Sanskrit "Ṛta", a fundamental Vedic concept dealing with the principle of the cosmic order (Panikkar, 2001; Holdrege, 2004). A central purpose of rituals concerns ordering of events, places and times, and their separation into the dimensions of Sacred and Profane (Eliade, 1959; Durkheim, 1963; Turner, 1982; Dulaney and Fiske, 1994). In this connection, rituals imply order and predictability, being "triggered" under anxiety-provoking conditions of uncertainty (Malinowski, 1922). Rituals, at whatever level of phylogeny, make the world orderly, so that behavior (be it in animals, individuals or communities) may be better oriented, coordinated and so controlled (Wallace, 1966). Regardless to the occasions for ritualized behavior (concerning life-stages or seasonal changes or unexpected contingences, such as illnesses or misfortune), rituals guarantee the stable order of the world or prevent a possible perturbation of the pre-constituted order. In so doing, rituals contribute to control the right course of natural and human events. Ultimately, ritual acts, with its intrinsic "performative" (i.e. formative and transformative) power (Tambiah, 1985), to maintain the homeostasis (i.e. the environmental stable condition and equilibrium) of human life-stages (rites of passage) and natural (seasonal and cosmic) cycles (Dulaney and Fiske, 1994). The persistent drive to ritualization in humans ("the ritual mind" according to Jones (2013)) may have been enhanced by the advent of symbolic conscience (Tattersall, 2017) that widened the concept of environment to the entire universe, with the emerging "cultural" problem to turn an unpredictable chaos into an ordered cosmos.

3.2. Intra-specific communication and group cohesion

With regard to intra-specific communication, through an exaptation phenomenon, habitual patterns that, for example originally served the function of body maintenance, acquire a communicative value, thus appearing as exaggerated copies of the original pragmatic ones. Collective rituals, exactly like in animal kingdom, promote a sense of connection within the group (Jones, 2013). A crucial mode of ritual cohesion is synchronized physical action that favors cooperation, shared intentionality (Reddish et al., 2013), intimate communicative and emotional bonding (Whitehouse, 2004). Proximate physiological mechanisms are yet unknown, but neuro-endocrine system could play a part. Particularly, oxytocin is critically involved in affiliative processes, enhancing prosocial interactions (Ross and Young, 2009). Moreover, oxytocin would exert a role in emergence and salience of "spirituality" (i.e. the belief in a meaningful life pervaded by a sense of connection to a Higher Power, the world or both) (van Cappellen et al., 2016). In human cultures, ritual synchronization facilitates the circulation and renovation of symbolic representations and myths (Eliade, 1948; Durkheim, 1963), promoting the consolidation of the "sacred values" of community (Ginges et al., 2007). Nevertheless, although myths and rituals are deeply intertwined, rituals remain an independent phenomenon, inherently compelling, pre-linguistic and more fundamental than myth and symbolic conscience (Staal, 1989; Burkert, 1998).

To sum up, human collective rituals would serve the function of increasing stability and predictability of the environment as well as connecting social groups, thus promoting the circulation of values and beliefs.

4. Psycho(patho)logy of rituals

Psychopathology may represent a favored viewpoint from which to deepen the phylogenetic role of rituals, since its special position at the crossing point of biological and cultural determinants (Turbott, 1997). Besides, a normal function or behavior may be highlighted by means of its corresponding psychopathological condition (Nesse and Stein, 2012).

Rituals are normally present in children to the point to be considered part of normal development (Graham, 1991; Barker, 1995),

starting at age two with a peak in middle childhood (Boyer and Lyenard, 2006). Contents and formal features are remarkably similar to pathological compulsions (Zor et al., 2009). This would support the hypothesis of a continuity between normal and pathological compulsions (Muris et al., 1997; Rassin et al., 1999). The most frequent themes in children are about orderliness and "just-right" household routines, with a strong tendency to magical thought (Turbott, 1997). Moreover, rituals tend to increase during particular phases in the lifetime, particularly pregnancy, motherhood and fatherhood, significantly concerning contamination or aggressive themes with related compulsions of washing and cleaning or of control (Abramowitz et al., 2003).

Noteworthy, compulsive rituals do not differ across the cultural groups (Zohar and Felz, 2001). The invariance across cultures would support the hypothesis that compulsions represent innate, pre-programmed behaviors inappropriately or excessively "released" in psychopathological conditions (Rapoport et al., 1994).

4.1. Psychopathology of OCD

In psychopathology, rituals of OCD are described as compulsions. According to the current diagnostic systems (DSM-5) (American Psychiatric Association, 2013), compulsions are repetitive behaviors that the individual feels driven to perform in response to an obsession or according to rules that must be applied rigidly. Therefore, unlike stereotypies, compulsions present a more complex motor and cognitive structure; the individual usually perceives them as intrusive and unwanted causing significant distress and functional impairment.

Recent studies confirm a dimensional architecture of OCD. The main symptom dimensions are: 1) symmetry obsessions with counting, ordering and repeating compulsions; 2) contamination obsessions with washing and cleaning compulsions; 3) hoarding compulsions; 4) aggressive obsessions with checking compulsions; 5) sexual and religious obsessions (Barahona-Corrêa et al., 2015).

Main symptom clusters concern ordinary or physiological acts (such as cleaning or washing) with a high evolutionary significance. Other symptoms, especially those concerned with ordering and arranging to achieve symmetry, appear to reflect a need to feel the environment "right" (Fineberg et al., 2018). Ethological and psychopathological studies have highlighted the striking similarities between animal habitual behavior and both human normal behaviors and pathological compulsions (Lorenz, 1966; Insel, 1988; Eilam, 2015). Likewise, several authors have emphasised the similarity in form and contents between compulsions and cultural rituals (Freud, 1961; Dulaney and Fiske, 1994).

Human ritualized behavior is present in different contexts (precautionary behavior, social behavior and psychopathology). Independently from the context, ritualized behavioral pattern is characterized by redundancy (superfluous actions that are non-functional for the achievement of a goal), repetitiveness (recurrent behaviors or utterances) and rigidity (emphasis on fidelity and invariance) (Lang et al., 2015). Moreover, compulsions are invariably inscribed into a precise spatio-temporal order (Eilam et al., 2006). Like both animal and cultural rituals, the focus of attention in compulsions is directed to the formal structure of the performance (Boyer and Lyenard, 2006; Eilam, 2015). That is, cognitive efforts are focused on the idiosyncratic "rules" of ritual, such as the number of repetitions, the details and the particular direction of the gestures and so on, even though compulsions are perceived as ego-dystonic (i.e. experienced by the subject as intrusive and unwanted or clearly absurd).

Different evolutionary hypotheses of OCD have been proposed: OCD has been related to a disruption of a specific "psychological immune system" (Abed and de Pauw, 1998), with compulsions conceived as a risk-avoidance behavior. Szechtman and Woody (2004) hypothesize an over-expression of a "security-motivation system" in OCD, evolved to monitor external signals of particular kinds of potential danger. Based on a similar evolutionary background, Boyer and Lyenard (2006) have

connected obsessions and compulsions to a "potential hazard repertoire" and a "precaution repertoire" respectively; that is, compulsions would be a species-specific, precaution-related behavior selected to prevent recurrent threats to fitness in ancestral environments.

Independently from the evolutionary model adopted, human ritualization appears to be triggered by uncertainty and unpredictability-related anxiety (Hirsh et al., 2012); that is, rituals would be performed for reducing a "high-entropy state" (e.g. a complex, uncontrollable or unpredictable situation), in order to regain a feeling of control and stability. In this connection, individual human rituals as well as psychopathological compulsions would deal with an anxiolytic feeling of stability and controllability of the environment. From the subjective perspective of the obsessive patient, compulsive rituals are performed to contrast a pervasive feeling of lack of order or "formlessness" (*an-eidos*) (von Gebsattel, 1938; Straus, 1987). This fear of "disorder" may be subjectively felt as spatial asymmetry (at the level of physical environment), pollution (organic environment) or moral impurity (at the level of symbolic conscience).

4.2. OCD comorbidity

Compulsions are not limited to OCD spectrum disorders but encompass different psychiatric conditions (Rapoport et al., 1994). Particularly, they occur in different neurodevelopmental disorders: OCS are major features of some autism spectrum disorders and they are highly comorbid with attention deficit hyperactivity disorder (ADHD) (Brem et al., 2014). Moreover, compulsions frequently occur in neuropsychiatric syndromes (Tourette's syndrome, post-encephalitic Parkinson's disease, mental retardation, dementia) (Turbott, 1997).

More generally, motor abnormalities, including stereotypies (defined as voluntary, highly repetitive and purposeless abnormal movements) represent (like other movement disorders, such as dyskinesias and catatonic-like signs) a relatively distinct neurobehavioral dimension, intrinsic to schizophrenia spectrum disorders, closely related to the underlying neurodevelopmental substrate (Walker and Lewine, 1990) and preceding the onset of psychosis (Compton et al., 2015).

Interestingly, OCD and obsessive-compulsive symptoms (OCS) are highly comorbid with both major endogenous psychoses, Bipolar Disorder (BD) and Schizophrenia (SCZ): lifetime prevalence of BD in OCD patients is up to 21.5%, while co-morbid OCD is diagnosed in 8–32% of patients with SCZ (Tonna et al., 2015a). Moreover, early-onset OCD often precedes the clinical onset of psychosis, significantly increasing risk for both BD and SCZ (Cederlöf et al., 2015).

In SCZ, OC and psychotic symptom dimensions, though independent from each other, tend to co- aggregate into complex symptom phenomena, with OCS "encapsulated" in delusional constructs. For example, compulsions may be linked to delusional themes or sustained by auditory hallucinations (Porto et al., 1997; Tonna et al., 2016a). This tendency reminds in anthropology the myth-ritual complexes (D'Aquili, 1983), where mythological constructs are inextricably embedded in ritualistic behavior. Interestingly, "schizo-obsessive" patients display a ritualistic behavior similar of that of "pure" OCD patients but they differ from OCD with respect to spatial behavior. In fact, OCD patients are more stationary when performing motor tasks (with restricted spatial motor behavior as a reflection of the high concentration in performing compulsions) whereas "schizo-obsessive" patients are much more mobile, wandering over a large area. In other words, SCZ−OCD comorbidity seem to combine a specific spatial behavior from both disorders: the addition and repetition of acts typical of OCD with more extensive exploratory behavior reminiscent of SCZ (Gershoni et al., 2014).

OCS have a significant impact on global functioning in schizophrenia. Particularly, mild OCS contribute to higher levels of functioning in schizophrenic patients with low levels of disorganization (Tonna et al., 2016b, 2016c). That is, rituals and compulsions may confer a certain functional order and stability, able to counterbalance the functional impairment sustained by the underlying thought and behavioral disorganization process. This psychopathological finding is in line with the "homeostatic function" of rituals from both ethological and anthropological perspective.

Moreover, growing evidence (de Silva and Marks, 1999; Mathews et al., 2008; Briggs and Price, 2009; Miller and Brock, 2017) suggests a strong association between different types of childhood trauma (emotional abuse and neglect) and the onset of OCS. A link between childhood trauma and "obsessive neurosis" was first postulated by Freud (1913). The mechanism through which trauma exposure affects severity of OCS is not understood yet. Nevertheless, it has been hypothesized that in predisposing individuals (e.g. with pre-existing genetic and neurobiological vulnerabilities) trauma may exacerbate the urge to engage in a compulsive behavior as a way to escape the intrusive-trauma-related imaginery, negative emotions and anxiety (Miller and Brock, 2017).

Altogether, OCS would emerge as an abnormal and invalidating ritualized behavior due to a pathological feeling of uncertainty and unpredictability. On the other hand, based on individual neurobiological vulnerabilities, psychopathological compulsive behavior might also reveal its original ordering and hyper-controlling function, counterbalancing an underlying "high-entropy state" due to a biological as well as to a higher-order level (psychological or sociocultural) disorganizing process (Kendler, 2005).

5. Neurobiology

5.1. Invertebrate animal studies

In invertebrates, rhythmic and repetitive behaviors are produced by specific central pattern generators (CPGs). CPGs are circuits able to initiate rhythmic motor patterns even in the absence of timing cues from sensory neurons or other extrinsic inputs. They are fundamental to generate organized and repetitive behaviors such as those underlying feeding, locomotion and respiration (Selverston, 2010). CPG circuits can be massively reconfigured by modulatory neurons and neuromodulatory substances such that different outputs can be produced by the same circuit elements, conferring behavioral flexibility as well as stability (Marder et al., 2005). In addition, modulators often directly mediate the interactions between functionally related CPGs (Dickinson, 2006). Therefore, far from being rigid and stereotyped, innate behavior is subject to modulation by internal states (e.g. satiety state) and external context of the stimuli (environmental cues). Context-dependent modulation is particularly well described for fruit flies. For example, male courtship in Drosophila is modulated by olfactory receptors (indicating the presence of food) to sustain the progeny (Grosjean et al., 2011). This inbuilt behavioral flexibility allows animals to prepare appropriate behavioral responses to stimuli and represent the basis for more complex behavior, such as learning and social behavior (Su and Wang, 2014). Such neuro-modulatory control pathways are highly conserved in vertebrates (e.g. with an important role in enabling spinal cord and brainstem circuits to generate rhythmic motor patterns) (Marder and Bucher, 2001).

5.2. Vertebrate animal studies

In vertebrates, a broad array of repetitive behaviors engages neural circuits interconnecting the neocortex with the striatum and related regions of basal ganglia (the cortico-striato-thalamocortical circuitry – CSTC). Particularly, basal ganglia circuits appear to operate in different types of cognitive and motor actions, exerting a primary role in the acquisition of repetitive behaviors and habits. Consistently, basal ganglia loops appear over-expressed in disorders producing repetitive thoughts and behaviors (Graybiel, 2008).

Growing evidence confirms the role of striatum in the acquisition of habitual motor patterns in rodents (Thorn et al., 2010). Particularly, in

mammals a dynamic competition is thought to occur between dorsomedial striatum (DMS) where intentional goal-directed actions are encoded, and dorsolateral striatum (DLS), where they are transformed into habitual automated responses. The reconfiguration of DLS circuit properties responsible for habit formation is modulated by interneuron plasticity on the striatal output (particularly involving a single class of interneuron, the "fast-spiking interneurons") (Fino and Venance, 2011; O'Hare et al., 2017).

In rodent experiments, habits can be defined as being performed not in relation to a current or future goal but rather in relation to a previous goal and the antecedent behavior that most successfully led to achieve the goal. Thus, goal-directed behavior are purposeful, "action-outcome" behaviors whereas habits are learned, automatic "stimulus-response" behaviors (Dickinson, 1985). Of course, the distinction based on the experiments between "action-outcome" vs "stimulus response" system is not absolute (Faure et al., 2005). Rather, there is a dynamic balance between control systems governing flexible cognitive control and more automatic control of behavioral responses (Daw et al., 2005). The gradient in striatal activity does not move "in toto" from one side to another; rather, activity can occur simultaneously in multiple cortico-basal ganglia loops, with dynamic shifts in cortical and striatal regions underlying the transition from goal-directed to habitual behavior (Graybiel, 2008).

As above seen, habitual behaviors are performed as a routine response to specific environmental triggers but, once provoked, are typically insensible to changes in environmental contingency (Fineberg et al., 2018). That is, habitual action steps are typically released as an entire behavioral episode once the habit is well engrained. This characteristic expression of an entire sequential behavior extends to stereotypes and rituals, including cultural rituals in humans, as well as psychopathological compulsions. Neural mechanisms involved in determining such extended, "incapsulated" behavior are not understood. Nevertheless, studies in monkeys (Fujii and Graybiel, 2003) and in rodents (Jog et al., 1999; Barnes et al., 2005) have shown heightened neural responses in sensorimotor striatum related to the first and last movements of the sequence, as though marking the boundaries of the habitual action sequences. When habitual motor pattern is encoded and "packaged" as a unit ready for expression, the boundaries of the unit are marked and the behavioral steps unfold from the first to the last boundary marker (Graybiel, 2008).

Altogether, cortico-basal ganglia loops are engaged in different types of repetitive behavior in vertebrates, with a gradient in flexibility, repetitiveness and automaticity from pure automatic and highly repetitive stereotypes to more complex and flexible habitual behavior. Rituals would represent the endpoint of this process from pure automaticity to full conscious control.

Interestingly, works in primates, rodents and lamprey have shown that the organization of the basal ganglia has been highly conserved throughout vertebrate phylogeny. The basal ganglia structures developed most likely to control basic patterns of behaviors, such as initiation of locomotion, steering, eye movements and feeding. In this connection, different modules within the basal ganglia are responsible for controlling different motor programs. During vertebrate evolution, this modular organization has increased in parallel to the evolution of new patterns of behavior (Grillner et al., 2013). Therefore, whereas the lamprey and "lower" vertebrates have a very limited behavioral repertoire and a correspondingly limited number of modules, mammals show an extensive and varied set of motor behaviors. Of course, during evolution from amphibians to reptiles, the elaboration of pallial-striatal connectivity may have enhanced behavioral flexibility. The expansion of cortical-striatal connectivity continued in mammals, becoming a critical point in evolutionary increases in behavioral flexibility and decision-making processes (Lee et al., 2015). In a remarkably similar way, an increasing connectivity in the hyperstriatum ventrale and neostriatum enhanced behavioral plasticity and innovation in birds (Lefebvre et al., 2004).

Growing evidence suggests a prominent role of basal ganglia also in the control and modulation of ritualized social behaviors and communication in both animals and humans. Bird song learning critically depends on a forebrain circuit that corresponds to a cortico-basal ganglia loop in mammals (Olveczky et al., 2005; Kao and Brainard, 2006). In humans the striatum and associated cortico-basal ganglia loops appear to be involved in human language (Lieberman et al., 2004; Crinion et al., 2006). Therefore, it is possible to hypothesize a role of cortico-basal ganglia circuits also in synchronized, communicative behavior typical of human collective rituals.

Altogether, basal ganglia exert a crucial role in the regulation of daily master routines and sub-routines from reptilians to humans, being responsible for 'species-typical' behaviors, which are present in aggression, dominance, territoriality, and ritual displays (MacLean, 2000; Ploog, 2003). Moreover, basal ganglia would be involved in ritualized social behaviors and intra-group communication in vertebrates.

5.3. Animal models of OCD-like behavior

Animal models of OC-spectrum symptoms were originally generated by employing either behavioral conditioning, pharmacological treatment or physical manipulation (Alonso et al., 2015). These studies converge on the fundamental contribution of corticostriatal circuitry in OCD-like symptoms, in keeping with the growing clinical literature (Burguière et al., 2015).

A central question to modeling OCD in animals is whether it is possible to characterize motor behavior not simply as a stereotyped, automated phenomenon but as representing an underlying cognitive-affective alteration (Wolmarans et al., 2018).

Animal models show a gradient from more "ritualized" behaviors (in which higher cognitive efforts are directed to the correct execution of the task) and more stereotyped and automated behaviors. Of course, subjective features of OCD, like obsessions or mental compulsions, are not accessible through animal models (Eilam et al., 2006). Nevertheless, models based on quinpirole-induced compulsive checking (referring to the behavioral changes in rats after chronic treatment with the D2/D3 dopamine agonist quinpirole) have shown compulsive-like features (distinguishable from "pure" stereotypies) in terms of cognitive focalization on the act itself and loss of automaticity. This induced compulsive-like performance has been interpreted "as parallel to the repeated compulsive rituals that OCD patients execute in response to an obsessive thought or idea" (Eilam et al., 2011). Similarly, behavioral animal models of OCD, like increased marble burying (based on the natural rodent behavior of burying noxious or harmless objects) or excessive nest building behavior seem to reflect a cognitive foundation. In fact, they implicate a reason for compulsivity, i.e. concerning about correctness of acts and "just right" perceptions (Wolmarans et al., 2016), which would be underpinned by CSTC pathways (Leckman et al., 1994; Monteiro and Feng, 2016).

Essentially, compulsive-like behavior in animal models presents the following features: 1) it varies in frequency and intensity within and between subjects variance; 2) it is resistant to behavioral sensitization; 3) it is repetitive, persistent and time consuming; 4) it is characterized by social deficits (Wolmarans et al., 2018).

In general, the more animal models have compulsive-like features, the more they show the attributes of highly motivated performance (i.e. with higher cognitive efforts) but without apparent satiation (Szechtman et al., 2017).

For animal models of OCD, a fundamental issue is to demonstrate a selective alleviation of OCD-like symptoms by administration of non-selective serotonin reuptake inhibitors (SRIs) (the principal anti-obsessive pharmacological treatment in humans), as well as the demonstration of a lack of effect of drugs such as non-serotoninergic antidepressants or benzodiazepines, which are not effective in OCD. Moreover, since in OCD patients SRIs administration is effective only some after weeks of treatment, beneficial effects should be achieved

after chronic (versus acute) administration (Alonso et al., 2015). Actually, various animal models (such as non-nutritive chewing, grooming, shifting/digging in bedding, or the nest building behavior) have confirmed the importance of the 5-HT system in the neurobiology and treatment of OCD with a successful response to chronic administration of high-doses SRIs (Korff and Harvey, 2006; Monteiro and Feng, 2016; Fineberg et al., 2018).

5.4. Neurobiology of OCD

Distinct, parallel and highly conserved neural systems within the cortico-striato-thalamocortical circuitry (CSTC) underlie the dimensional structure of OCD (Mataix-Cols et al., 2004). Particularly, discrete neural systems appear to mediate the expression of different symptoms. The neuroanatomic proximity within the fronto-striato-thalamic loops and the fact that they are "open" circuits (i.e. allowing connections between various sub-structures) (Tibbo and Warneke, 1999) may explain the frequent coexistence of different symptom dimensions. These circuits lie at the crossing point of widespread cortico-subcortical loops involved in the pathophysiology of both BD and SCZ. Specifically, BD is mostly related with hypoactivity in orbitofrontal cortex (OFC) (i.e. decision making, impulse control) and in dorsolateral prefrontal cortex (DLPFC) (i.e. planning, attentional set shifting), while OCD mainly presents hyperactivity of OFC with deficit in emotional processing (Ekman et al., 2010). Schizophrenia shares similar cortical-subcortical pathways with specific patterns of DLPFC functional impairment, affecting working memory (Goldman-Rakic, 1994; Lewis et al., 2004). Fronto-striatal dysconnectivity within overlapping cortical–subcortical circuits may partially explain the frequent co-occurrence of OCS during the course of both BD and SCZ (Tonna et al., 2015a, b) as well as the tendency of OC and delusional symptoms to co-aggregate into unique psychopathological complexes (Porto et al., 1997).

The evolutionary conserved cortical-striatal-thalamic loops along vertebrate phylogeny, despite the huge differences in connectivity across species (with the increasing role of prefrontal cortical areas in modulating sub-cortical circuits in primates (Marchesi et al., 2009; Monteiro and Feng, 2016) permits a parallel between OCD and habitual behavior in animals.

Actual pathophysiological models of OCD agree on the crucial role of the caudate nucleus, regardless to a primary (subcortical model) or a secondary (cortical model) involvement (Barahona-Corrêa et al., 2015). Particularly, it has been hypothesized a disruption of the caudate's "filter" in the activation and maintenance of highly conservative behavioral and cognitive patterns (Baxter et al., 1992; Fineberg et al., 2018).

Therefore, compulsions would result from an excessive release of habitual, cyclic, species-specific, action strategies (Thorn et al., 2010) due to an exaggerated shift from goal-directed to habitual behavioral control mediated by a dysfunction within the dorsal striatum (Gillan et al., 2014; Fineberg et al., 2018). Interestingly, an unbalance between goal-directed and habitual behavior sustained by frontostriatal dysconnectivity has also been found in unaffected first-degree relatives of OCD patients, representing a candidate endophenotype for OCD (Vaghi et al., 2017).

The caudate nucleus is under the prevailing influence of the ventromedial prefrontal cortex (vmPFC). The vmPFC plays a complex role in fear learning and safety signaling in mammals, including humans, and it is closely involved in integrating the evaluative processing of environmental cues with flexible behavior (Fineberg et al., 2018). Studies in rats have demonstrated a role of vmPFC in recalling a previously learned extinction fear (Quirk et al., 2000). Moreover, medial prefrontal cortex is important in the control of checking via its role in uncertainty processing; consistently its dysfunction is implicated in excessive checking behavior in rats (D'Angelo et al., 2017).

Abnormal vmPFC activation has been implicated in impaired fear retention in OCD (Milad et al., 2013). Particularly, it has been

hypothesized a dysfunctional vmPFC safety signalling in OCD that potentially undermines explicit contingency knowledge, leading to the failure to flexibly update fear responses and the persistence of rigid habitual compulsive activity (Apergis-Schoute et al., 2017). In other words, the inability to update threat estimation, with the consequent perception of environmental unpredictability lead to the generation of habit behavior, expressed in ritualized form.

In general, prefrontal cortex has long been implicated in inhibition of inappropriate responses in mammals (Quirk et al., 2000) via a top-down inhibitory control over sub-cortical structures (basal ganglia) (Fineberg et al., 2018). Particularly, the orbital and medial prefrontal regions, though overlapping functional and organization features, are involved in partially distinct 'orbital' and 'medial' prefrontal networks that differ in their intrinsic pattern of cortico-cortical connections and also in their connections with sensory, limbic, striato-thalamic and visceromotor structures in other parts of the brain (Ongür and Price, 2000). OFC has been strongly implicated in OCD pathophysiology (Manning, 2016): OFC is important in behavioral flexibility after negative feedback (reversal learning) in rats (Ragozzino, 2007). Moreover, hyperactivity in OFC-striatal pathways induces augmented sensitivity to initial trigger stimuli (start signal) or to deficiency in motivation to break the initiated behavioral ritual (stop signal) in mice with perseverative grooming behavior (Monteiro and Feng, 2016). Human functional imaging data suggest OFC hyperactivity in patients with OCD. These data are corroborated by the finding of OFC dysregulation also in unaffected relatives of OCD patients (Chamberlain et al., 2008).

Taken together, OCD would be associated to a deficient top-down inhibitory control in prefrontal cortex nodes (vmPFC and OFC), coupled with a shift from flexible-contingency behavior to excess habit generation and mediated by dysfunction within the striatum (Fineberg et al., 2018). This is consistent with recent results from neuroimaging studies showing consistent gray matter volume alterations in prefrontal-striatal circuitry with greater striatal volume and reduced prefrontal grey matter volume in OCD adults (Hu et al., 2017).

6. Formal structure of rituals

Habitual action sequences, relatively invariant and mainly dependent on sensorimotor striatum, are built on single action-units, each triggered by the antecedent action rather than by environmental stimuli. Therefore, they lie on reverberant and self-sustaining cycles (Ostlund et al., 2009; Dezfouli and Balleine, 2013), disconnected from environmental contingences (Fineberg et al., 2018).

The elementary motor units of habitual behavior have been divided into functional/common acts (mandatory for task performance and rendering behavior its rigidity and pragmatism) and non-functional/idiosyncratic acts (unnecessary or even irrelevant for the task, but conferring variability, plasticity and individualism of behavior) (Zor et al., 2009; Eilam, 2015).

An important feature of habitual behavior is its specific spatio-temporal structure (Eilam et al., 2006; Zor et al., 2009). Space is conceived as a specific set of places where a specific set of acts is performed at a specific time. Thus, whenever ritual is performed, the environment is remodeled through precise spatial and temporal criteria.

Rituals maintain the circular and spatio-temporal structure of habitual behavior: first, rituals, like habits, are motor sequences constructed on and fragmented into single action-units, within a reverberant cycle. The beginning of the action may be triggered by external stimuli but once activated, the motor sequence is self-sustaining, marking its compelling character (Tambiah, 1985; Dulaney and Fiske, 1994) as well as the sense of lack of task completion or "incompleteness", typical of OCD patients (Rapoport, 1989; Ecker and Gönner, 2008).

Second, rituals, like habits, are inscribed into precise spatio-temporal parameters. The spatio-temporal structure of rituals has been

described in animals (Hediger, 1964), in psychopathological compulsions (Eilam et al., 2006) and in cultural rituals (Eliade, 1959).This implies a re-organization of the environment where rituals are performed through a super-imposed order and control (Zor et al., 2009).

Rooted in this "basic structure", ritualization occurs through two combined mechanisms:

1) The excessive performance of non-functional acts, considered as the core process of ritualization (Zor et al., 2009).That is, when a behavior acquires a ritual form, its performance presents a high rate of repetition and exaggeration through an inflated performance of unnecessary acts. In this respect, habitual action-units are not simply non-functionally repeated, but also "exapted" into an ex-aggerated, magnified form. The result is a reduced functionality in terms of task completion (Zor et al., 2009) and a detachment from its global function (Eilam, 2015) with a lack of pragmatic goal (goal demotion) (Boyer and Lyenard, 2006).

2) Direction of locus of attention to the task (Eilam et al., 2006; Krátký et al., 2016); that is, cognitive efforts are redirected to the "just right" of the acts or the "script" of the performance. Therefore, motor performance loses its automaticity with hyper-attention on the formal structure of the behavior, with special focus on the smaller units of the action flow (action parsing) (Boyer and Lyenard, 2006).

Psychopathological compulsions may be conceived as ritualized habitual behavior in that, like habits, they are characterized by repetitive action sequences that become disconnected from the prevailing environmental contingencies and lack an obvious relationship to the overall goal of the activity, but, like rituals, they lose automaticity in favor of hyper-attention to the "precise" execution.

To sum up, we hypothesize that rituals developed from habitual behavior through an increase of non-functional acts (enhancing behavioral flexibility to environmental changes) with loss of automaticity and redirection of attention to the performance itself.

7. Discussion

Every attempt to link together a wide range of phenomena from different disciplinary fields may be exposed to the criticism of reductionism (Turbott, 1997). Nonetheless, it is intriguing to hypothesize a continuity among behaviors so strikingly similar in forms and contents and extensively diffused in nature, psychopathology and culture. Even though one can assume that different evolutionary trajectories may have converged into apparently comparable manifestations, the present contribution would suggest that indeed remote fundamental links connect the various types of ritual. In other words, at least in vertebrate phylogeny, similarity may be better explained in terms of homology:

1) Face validity: the same formal structure underlies animal, psycho-pathological and cultural rituals. Moreover, few and invariant contents cut across different ritual manifestations, insisting on ordinary or physiological acts or actions (such as ordering, checking and re-arranging) aimed at environmental constancy.

2) Construct validity: The neuro-biological substrate of rituals in vertebrates lies on the cortico-striato-thalamocortical circuitry (CSTC), which is focused on the basal ganglia; structures that are highly conserved and implied in daily routines and habits. Moreover, animal models of OCD-like behavior would confirm a similarity in neural systems implicated and behavioral phenotypes to human compulsions.

3) Predictive validity: different animal ritualized behaviors are used as OCD models and respond to the same OCD therapeutic agents (serotoninergic drugs) (Monteiro and Feng, 2016; Fineberg et al., 2018).

It is intriguing to hypothesize that homology of ritual behavior may be backdated up to invertebrate phylogeny. If we consider a hierarchical level of homology, behaviors can be homologized at the level of the structural bases that allow that behavior to be displayed (e.g. the basal ganglia for rituals in vertebrates), at the level of the neural control of the behavior or at the level of the genetic pathways of a behavior (Hall, 2013). We know that developmental genes such as *hox* genes have a highly functionally conserved role throughout phylogeny (e.g. specifying anterior-posterior morphology in both arthropods and chordates) (Burke et al., 1995; Catela et al., 2016). Homologous genes at the level of DNA sequence might influence similar categories of behaviors across taxa (Reaume and Sokolowski, 2011). In other words, the same genes could be implied to build the potential for specific behaviors in both invertebrates and vertebrates (Baker et al., 2001).

The backbone of ritual performance lies on the circular and spatio-temporal structure of habitual behavior, displaced from its original context and "exapted" for a different purpose. Ritualization develops when the action flow is disrupted by high repetition of non-functional acts and motor performance loses its automaticity with hyper-attention to the act itself. Moreover, the deviation of cognitive efforts on the act (rather than on the function) implies a further exaggeration of formal features (in terms of redundancy, repetitiveness and so on).The result is a complete detachment from the original pragmatic goal.

If rituals imply non-functionality (and, at some extent, even exposure to threats and predators) what can we infer about its evolutionary meaning?

Throughout invertebrate and vertebrate phylogeny, the adjustment to environmental unpredictability implies a shift from habitual and automated processes to an enhanced focalization and control on the performance with loss of automaticity.

It has been suggested (Eilam et al., 2011) that the redundancy of non-functional acts reduces anxiety giving a feeling of controllability and predictability. Non-functional acts guarantee behavioral plasticity to fit the situation, preventing automatic performance (Zor et al., 2009; Eilam, 2015). Their inflated repetition would have been promoted to enhance behavioral flexibility in order to face environmental unpredictability. At the same time, the redirection of attention to the formal structure of the performance gives itself a sense of control and order.

We hypothesize that rituals, whether animal, human or cultural, are performed to create order, stability, regularity and ultimately predictability of the environment (Fiske and Haslam, rons..01.023, 2011Fiske and Haslam, 1997). This ordering and stabilizing function, perhaps still present in invertebrate phylogeny, may be traced at any level of vertebrate evolution: in animal (from "lower" vertebrates to mammals) ritual behavior (Serruya and Eilam, 1996), in human daily-life rituals and, distorted and magnified, in psychopathological compulsions. In that sense, OCD, like other psychopathological conditions, may represent the hyper-expression of a normal, highly evolutionarily conserved "protective response" (Rapoport et al., 1994; Nesse and Stein, 2012). The function of controlling the environmental constancy is also conserved in human cultural rituals, performed to preserve the "right" order of human, nature and cosmic cycles (Wallace, 1966; Dulaney and Fiske, 1994). Rather, this phenomenon is particularly evident in collective cultural rituals, which have been consistently described as a "homeostatic" and adaptive response to ecological or social "dis-ordering" threats (Malinowski, 1922; Sosis and Handwerker, 2011).

Environmental unpredictability (either social or non-social) generates anxiety in both animals and humans (Foa et al., 1992; Palanza, 2001; Palanza and Parmigiani, 2017). Whenever there is a threat of uncontrollability and unpredictability, i.e. a potential "disorder", rituals are performed to maintain the pre-existing order, reducing anxiety. During the performance, attention is focused to the reordering sequence of ritual acts (repetition, specific number of procedural steps, time-specificity), which in turn, leads to the subjective perception of a "re-ordered" world (Legare and Souza, 2012). The result is to actually

achieve a change of state or do something effective (the so-called "performative" character of ritual acts and magical rites (Tambiah, 1985)). From a psychopathological perspective, this corresponds to obsessive "magical thought": "if I act in that specific way, everything's going to be fine".

The other important phylogenetic process of ritualization concerns intra-specific communicative cohesion, originated through Darwinian socio-sexual selection pressure (Darwin, 1871). In this regard, the repetition and exaggeration of ordinary acts for communication may have been promoted by social environmental selective pressures. Ritual motor synchronization of these "exapted" ordinary or maintenance acts, further promotes intra-group connection and intra-specific communication, essential to strengthen and regulate social bonds and, in human cultures, to circulate collective symbols and myths.

We want to emphasize that the "homeostatic" function of individual (non-social) and collective (social) rituals do not represent divergent evolutionary paths but share a common origin. In fact, both rituals are "aimed" to environmental control. In social animals (including humans) rituals promote communication and group cohesion thus predictability of social environment. Therefore, repetition of non-functional acts deals with environmental unpredictability in non-social contexts and further enhances communicative bonding in social contexts.

Our hypothesis of rituals (i.e. as an exaptation phenomenon from habitual behavior aimed at increasing environmental stability under conditions of unpredictability) is not in contrast with previous evolutionary models (Abed and de Pauw, 1998; Szechtman and Woody, 2004; Boyer and Lyenard, 2006). Rather, the concepts of "security motivation" or "precaution repertoire" systems may be included in such evolutionary background and contributes to explain the remarkable invariance and species-specificity of many "contents" of rituals (Dulaney and Fiske, 1994). However, the present model permits to trace a phylogenetic continuity of rituals through convergent interdisciplinary data (ethology, anthropology and psychopathology) and to explain an equal remarkable invariance of formal features of rituals.

The "gap" between biology and culture may be bridged through the assumption that culture, as "extended phenotype" (Dawkins, 1989), continues the ancient paths followed by biological evolution (Lévi-Strauss, 1958; Wickler and Seibt, 1991; Burkert, 1998). We suggest that the "ritual mind" (Jones, 2013), i.e. the widespread drive to ritualization typical of every culture, is biologically inherited and goes back to the phylogenetic roots of our species. This does not mean to underestimate the determinant role of culture in shaping human behavior and mind, due to the high plasticity of our brain (Palanza and Parmigiani, 2016). On the one hand, culture is rooted on nature; on the other, nature is expressed via culture by epigenetic mechanisms in a circular loop (Ridley, 2003).

Motor ritual behavior was the primary development in the evolutionary sequence, with language and symbolic meanings being secondarily superimposed (Glenberg and Gallese, 2012; Staal, 1989). Noteworthy, the basic invertebrate and vertebrate neuroscience is converging to a remarkable degree (Gelperin, 2017). From an evolutionary perspective, the basic principles of cellular, neural network and behavioral phenotypes (especially those concerned with fixed motor or action patterns which are essential components of rituals behaviors) appeared very early in the phylogeny of eukaryotic organisms (i.e. Cnidaria or Coelenterata) and were maintained and conserved congruent in vertebrates. Therefore, a unitary hypothesis of rituals permits to capture its evolutionary complexity and stratified structure from ritualized motor behavior up to the myth-ritual constructs with the advent of symbolic conscience (Tattersall, 2017).

Lastly, we have attempted to bring together data from a variety of disciplines to address the question of whether a continuity may exist in ritual behavior; we would be the first to admit that we have not been exhaustive in all the areas we have touched on. We hope that this work will stimulate interdisciplinary research to contribute to the discussion.

Concluding, ubiquitously rituals, following its biological constraints, work on maintaining a predictable and ordered (thus safe) environment (social and non-social), facing anxiety-related unpredictability. In doing so, rituals exert a "homeostatic" function, reassuring that animal and human cycles carry out according to the "right" order.

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