UNIVERSITA' DEGLI STUDI DI MODENA E REGGIO EMILIA

DOTTORATO DI RICERCA IN NEUROSCIENZE

IN CONVENZIONE CON L'UNIVERSITA' DEGLI STUDI DI PARMA

CICLO XXXII

The "ritual mind": an interdisciplinary perspective

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ANNO ACCADEMICO 2018-2019

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Proximate and ultimate causes of ritual behavior

1. Introduction

Rituals (e.g. play, agonistic and mating rituals) are a ubiquitous phenomenon in animals including humans and they conserve a strikingly similar formal structure. For this reason, ritualized behaviours generate interest across many, separate disciplines (ethology, anthropology, psychopathology). Surprisingly, there is no precise definition of "ritual" in any of the three fields that deal with its typical manifestation (Boyer and Lienard, 2006). The term "ritual" has been indifferently adopted to describe separate forms of repetitive behavior (such as stereotypies, fixed action patterns and habitual behaviour) in ethology (Payne, 1998). In anthropology, it is generally accepted the definition of a scripted, stereotypic form of collective actions (Gluckman, 1975). Therefore, a distinction of rituals from other forms of repetitive behavior is often not clear (Tonna et al., 2019). In this contribution, we will focus on the notion of "Ritualized Behavior", as a specific way of organizing the flow of behaviour, as first indicated by Rappaport (1979) and fruitfully developed in both anthropological and ethological fields (Liénard and Boyer, 2006; Eilam et al., 2006; Zor et al., 2009).

In many animals, ritualized behavior is the result of "exaptations" (Immelmann and Beer.1989). "Exaptation" is a term used in evolutionary biology to describe a trait shaped by natural selection for a particular adaptive function that has been co-opted for a new use and function (Gould and Vrba, 1982). Ethologists described the phenomenon of ritualization of behaviour as an evolutionary process by which an action or behavior pattern has lost its original function to become highly stereotyped and coopted for intraspecific social communication display (Lorenz, 1966). In humans, ritualized behavior (i.e. a highly stereotyped, repetitive pattern of behavior) are found across different cultural rituals (whether through religion, politics or the military) and characterizes many individual daily-life activities (Hobson, 2018; Eilam, 2015

1.1 The concept of Proximate and ultimate causes of behaviour

In the paper "Cause and effects in Biology", Ernst Mayr (1961) suggested that from the perspective of evolutionary biology, in order to understand the biological structures of organisms we must obtain both proximate (how they work) and ultimate (why they are made in that way) explanations. In "On Aims and Methods of Ethology", Niko Tinbergen (1963) pointed out that every fully formed feature of an organism, including any aspect of its behaviour, raises four different types of questions (known as the "Tinbergen's Four Questions"). Two of the questions are about proximate causes, i.e. the ontogenetic development of a biological trait and the mechanisms and structures through which that trait works to accomplish its function. The remaining two questions are about ultimate or evolutionary causes, i.e. the phylogenetic history of the trait and its adaptive significance (Nesse, 2018). The "four questions" are complementary: answers to all four are necessary for a complete biological explanation. From a theoretical point of view there have been debates (Tinbergen N. 1963) about the possibility to experimentally tackle the why questions (phylogenetic history and adaptive significance) because the "current function" of the behaviour might not be the same of the original one (Bateson and Laland, 2013) but the result of exaptation phenomena (Gould and Vrba, 1982).

In agreement with Tinbergen (1963), hypotheses on the adaptive significance of a given behavior generate, through the hypothetic deductive logic, experimentally testable predictions about the proximal mechanisms that should underlie the behavioral trait in order to fulfill its adaptive function (Palanza and Parmigiani, 1991; Parmigiani and Palanza, 1991). This approach could be applied to the study of ritualized behaviors, as it will help us to understand if animal and human ritualized behaviors are homoplastic (i.e. analogous, in that the similarities in behavioral traits are the result of convergent evolution due to similar environmental selective pressures) or homologous (i.e. the behavioural trait shares a common phylogenetic history).

Under this respect, ritual behavior, like every human and nonhuman animal behavior, is shaped by a complex interaction between genetic and cultural evolutionary processes within a specific environment, to the point that elucidating the relative contributions of genes, culture and environment to a behavioural phenotype can be very difficult (Legare, 2017; Creanza et al., 2017). The reciprocal action of biological and cultural selective pressures within a specific environment is referred to gene–culture coevolution (Feldman and Laland, 1996) or niche construction (Odling-Smee et al., 2013).

We suggest that only by means of an inter-disciplinary approach it is possible to grasp if there is an evolutionary continuum in terms of both proximal and ultimate causes of such apparently conservative behaviour (from biology to culture), which is so complex and time-consuming, motor and cognitive demanding and, above all, apparently purposeless.

Following Rappaport's classification (1971), in the present work, ritual behavior will be separated into ecological and social since its particular "adaptive significance" or "current utility" related to respectively the non-social or social environment where ritual is at work. Instead, the relationship between ritual behavior and symbolic activity will be discussed separately in agreement with the complexity and specificity of ritual phenomenon within human eco-cultural and developmental niches.

The hypothesis that will be developed is that an evolutionary continuity in ritual behavior exists, with proximal mechanisms based on specific formal features of motor pattern and with the adaptive significance dealing with ecological or social conditions of unpredictability.

2. Proximate mechanisms of ritualized behaviour

2.1 Formal structure

Tinbergen's "why" and "how" questions can be answered only with a precise definition of the formal features or the internal structure of a behavior. If attention is shifted to the specific characteristics of action flow, shared formal features of ritual behaviour may be discovered, cutting across different disciplines (Tonna et al., 2019).

In a previous work (Tonna et al., 2019) we have suggested that the action flow of ritual behavior presents specific and invariant characteristics: 1) the motor pattern is chunked into units of segmented action (Boyer and Liénard, 2006), which are inscribed into precise spatio-temporal parameters (Eilam et al., 2006; Zor et al., 2009) and within reverberant and self-sustaining cycles (Ostlund et al., 2009; Dezfouli and Balleine, 2013); 2) these action-units are rigidly repeated with a huge prevalence of non-functional acts (i.e. actions that are unnecessary or even irrelevant for the task) (Zor et al., 2009; Eilam, 2015); 3) the internal repetition and redundancy implies a loss of automaticity of the motor performance in favour of a cognitive focalization on the act itself (i.e. the rigid rules or the "script" of the performance), referred to as "thoughtfulness" (Eilam et al., 2006). The final outcome is a detachment from a pragmatic goal (*goal demotion*) and a special focus on the smaller units of the action flow (*action parsing*) (Boyer and Liénard P. 2006) with a complete disconnection from environmental contingences (Fineberg et al., 2018). Such loss of pragmatic purposes or "meaningless" of ritual is apparently in contrast with another typical feature of ritual behaviour, i.e. its compulsory character. That is, animal and human ritual acts are inherently compelling (Rappaport, 1979; Tambiah, 1985; Dulaney and Fiske, 1994; Boyer and Lienard, 2006).

With regard to their formal structure, compulsions in Obsessive-Compulsive Disorder (OCD) are indistinguishable from both ethological and anthropological descriptions of ritual behaviour (Tonna et al., 2019). In OCD compulsions, the process of ritualization is achieved through action segmentation, enhancement of non-necessary acts and loss of automaticity with focalization on the "correct" execution of the motor performance (the "just right" perception of the act) (Eilam, 2015) Moreover, the compulsory character is a main feature of OCD too, even though compulsions are generally ego-dystonic (i.e. experienced by the subject as intrusive and unwanted or clearly absurd). Regardless to their ego-dystonic character, OCD compulsions are often accompanied by a "magical thought" disposition ("if I act in that specific way, everything's going to be fine").

The rigidity of action flow is coupled with a striking “narrowness” of themes or contents expressed by ritual behavior. In ethological descriptions, rituals are built upon ordinary or physiological acts, displaced from their original pragmatic purpose and expressed in a distorted or magnified form. For example, through exaggeration and repetition, ordinary acts get divorced from its original pragmatic goal and “exapted” for a communicative value (Immelmann and Beer, 1989). Similarly, in human collective rituals habitual patterns that, for instance, originally served the function of body maintenance, acquire a symbolic value (Penner, 1992). The same narrowness of themes may be found in OCD compulsions (Mataix-Cols et al., 2004). The ordinary or physiological acts invariably recurring in ritual behavior typically concern the action cleansing or washing, checking the environment or delimiting space. This invariance is maintained across cultures and regardless to whether the ritual behaviour is individual or collective, psychopathological or part of normal development (Dulaney and Fiske, 1994; Maitaix-Cols et al., 2004; Lienard and Boyer, 2006). In animal rituals, these ordinary acts are generally represented by fixed-action patterns (FAPs) (Tinbergen, 1953) or habitual motor displays (Eilam, 2015).

FAPs are innate (pre-programmed) and “fixed” repetitive sequence of behaviors (Immelmann and Beer, 1989). That is, the highly predictable relationship between the external stimulus and response has been “genetically” fixed by natural and/or sexual selection

The ethological analysis of FAPs clearly show how their proximal mechanisms explain their adaptive function. Stereotyped genetically programmed FAPs and their innate releasing neural mechanisms are a fine adaptation to very predictable environmental stimuli (such as for example a potential mate as far as social environmental situations). These species-specific behaviors are correctly performed the first time an animal is exposed to the releasing stimulus, with a very little inter-individual variability. As innate genetically programmed behaviors, they represent the so-called “phylogenetic memory” of the species (Lorenz, 1966).

Conversely, in habitual behavior, the predictability of behavioral outcomes in a given environmental context is learned [20].

Actually, in both vertebrates and invertebrates, a continuity exists between innate and learned behavior. Even highly stereotyped patterns of behaviour, such as FAPs, maintain a certain plasticity, with motor performances showing both fixed and variable components. Behavioral flexibility is essential for short-term adjustment to changing environments (Keren et al., 2010). Plasticity of motor patterns is guaranteed by the presence of specific action-units, embedded within the action flow, which are unnecessary (i.e. non-functional or irrelevant for the task) and idiosyncratic (i.e. with a huge intra-individual variability) (Eilam, 2015). Unnecessary/idiosyncratic acts guarantee a certain flexibility by irregularly interrupting the automatic performance, thus enabling the performer to maintain the control over environmental changes (Keren et al., 2010). In other words, unnecessary acts prevent automated processing with no or minimal attention (Moors and de Houwe, 2006). In so doing, the motor sequence may be modifiable to fit the situation (Dumais, 1981), allowing the organism to test its environment and facilitating motor exploration necessary for learning (Brembs, 2011). Such context modulation of motor variability has been observed in both humans, underpinned by homologous basal ganglia circuits (Schmidt and Ding, 2014) and would be at work in both ecological and social contexts (see for example social modulation of songbird variability in zebra finch -Woolley et al., 2014-).

Conversely, medium and long-term behavioral adjustments to environmental changes are mediated by epigenetic processes. It is now clear that genomes are regulated to a large extent as a result of input from environmental events and experiences via epigenetic modifications shaping animal and human behaviors (Jensen, 2013). Such epigenetic mechanisms are also involved in multigenerational transmission and transgenerational inheritance of behavioural patterns (Szyf, 2015).

Altogether, ritual is an apparently highly conserved behavior built on ordinary acts (innate FAPs or learned habitual motor patterns), of which maintains important features (for example a specific spatio-temporal structure and a compulsory character). These “building blocks” however appear rearranged in a different form: often exaggerated or magnified, non-functionally repeated, heavily inflated with unnecessary acts and no more automatic. From an evolutionary perspective, these original patterns of behavior are “exapted” (i.e. functionally modified) and used in a different context.

2.2. Neurobiology

2.2.1 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).

2.2.2 Vertebrate animal studies

In vertebrates, a broad array of repetitive behaviors engage 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 achieving 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.

2.2.3 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) as well as the tendency of OC and delusional symptoms to co-aggregate into unique psychopathological complexes (Porto et al., 1997; Tonna et al., 2016a).

The evolutionarily 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 (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-Correa 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 (Aspergis-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).

Altogether, an evolutionary continuity may be traced, at least throughout vertebrate phylogeny (from lamprey to humans), with respect to the neural circuits underlying different types of repetitive, innate or learned, motor displays. Ritual behavior appears therefore as a multifaceted developmental process, “hardwired” in highly conserved neural pathways, but continuously remodelled by nongenetic factors, throughout the lifetime of the animal within ecological and developmental niches. Plastic behavioural responses to environmental change are particularly true in human cultural niches, which rituals contribute to shape and through which are shaped in a circular way.

Therefore, on the one hand ritual behavior incorporates evolutionarily highly conserved motor displays, which represent the action-units of ritual, but on the other, these action-units are rearranged in a novel, purposeless form. Which is the adaptive significance of such a behavior, which is so time consuming and apparently purposeless? The model here proposed is that ritual behavior through its proximal mechanisms (i.e, the non-automatic repetition of action-units displaced from their original context) is a response to unpredictable environmental conditions. Namely, ritual behaviour represents a coping response strategy to give order and control over the environment (both ecological and social).

3. Ultimate causes

Rituals, because of certain formal characteristics, are suitable for both communication and regulatory functions, through a process of reordering and simplification of ecological and social environments (Rappaport, 1971; Dulaney and Fiske, 1994). In a Darwinian perspective, the ecological function may be referred to natural selection (i.e. the selective pressure comes from an abiotic or biotic environment), whereas the social function may be referred to intra-sexual (i.e. competitive aggression for mates) or inter-sexual (i.e. mating strategies) selection. In social animals (even more so in humans), ecological and social order are interdependent phenomena, regulating unique socio-ecological niches.

3.1 Ecological function

Interestingly, in both invertebrates and vertebrates, the automaticity of the performance, as well as the repetitiveness and rigidity of a behavioural pattern, seem to be directly related to the levels of environmental predictability. That is, at increasing levels of anxiety-related uncertainty, behaviour becomes more repetitive and loses automaticity in favour of major cognitive control (Schleyer et al., 2013). The same mechanism has been observed in both vertebrates (Lorenz, 1966) (including humans - Lang, et al., 2015-) and invertebrates (Stürzl et al., 2016). The first observations are derived from classical ethology, where animal repetitive, apparently purposeless, ritual-like behaviors were described to be triggered whenever the uncontrollability and unpredictability of the context increase, for example in gooses when habitual routines are abruptly interrupted or usual paths are changed (Lorenz, 1966). Evocatively, Lorenz (1966) defined these behavioural adjustments as “proto-religious”.

The same mechanism is still present in invertebrates; for example, in Drosophila a shift from automated habitual behavior to non-automated, attentional behaviour occurs whenever uncertainty increases (Schleyer et al., 2013). The interruption of an automatic performance in favour of non-automatic, repetitive, adjustment behaviors (re-orientation flights) has been also demonstrated in wasps and bees (Stürzl et al., 2016). These repetitive, attentional behavioral patterns are constantly aimed at re-establishing a spatial representation of the environment when natural environment is no more predictable. In other words, whenever a "mismatch" occurs between habitual automatic behavior and surrounding environment, adjustment repetitive, non-automatic motor patterns are elicited to recreate a novel spatial rearrangement.

Animal models (for example marble-burying or nest building behaviour in mice) demonstrates that, at least in mammals, such non-automatic and repetitive motor patterns (which may be pharmacologically induced or behaviourally conditioned) share formal features typically referred as ritual-like or compulsive-like behaviors particularly, a "cognitive" foundation concerning about correctness of acts and "just right" perceptions (Wolmarans et al., 2016).

The non-pragmatic repetition of action-units, mostly non-functional acts, mediates the shift from more automated behaviour to attentional focalization on the act itself (i.e. its ritualization) (Zor et al., 2009), enabling the motor control and flexibility that is necessary for behavioral adjustment to changing circumstances (Keren et al., 2010). Across taxa, the non-automated repetition of non-functional acts is an adjustment behaviour with the aim of enhancing behavioural plasticity in conditions of environmental unpredictability (Eilam, 2015). Whenever ecological circumstances abruptly change, the automaticity of habitual behavior is interrupted in order to align behavioral response to the new environment. This is consistent with the "entropy model" of rituals (Hirsh et al., 2012; Lang et al., 2015; Krátký et al., 2016) , which proposes that when individuals face unpredictable situations, they experience a high-entropy state, characterized by a reduced ability to predict future states from the current one. In this respect, ritualized behavior would minimize internal entropy, regaining a fundamental need for order and control (Hobson et al., 2017; Sosis and Handweker, 2011). We propose that the first drive to ritualization appeared very early during evolution as a consequence of a mismatch between unexpectedly changed environmental conditions and prior automatic behavioural patterns, “triggering” an adjustment mechanism (based on non-automatic and highly repeated motor acts) aimed at regaining a novel environment-behavior homeostasis. Such adaptive mechanism is primarily a motor phenomenon, embracing vertebrate and invertebrate behavior, thus prior to cognitive adjustments.

It has been suggested that repetitive and rigid physical action have an “anxiolytic” effect for itself (Anderson and Shivakumar, 2013). Along with the progressive involvement of cortical control during phylogeny (and therefore, with the increasing role of cognition), other “higher” (i.e. cognitive) mechanisms may contribute to enhance the ritualization process. For example, in human individual (e.g. sport rituals) and collective rituals, during a motor task, 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). That is, the cognitive effort on the correctness of the “ordered” movements represents a signal to the self of one’s control over a situation. On the other hand, the focalization of cognition to the rigid rules of ritual may divert attention from negative emotions such as anxiety, uncertainty and stress (Hobson et al., 2018). In this connection, it has been hypothesized that the rigid repetition during ritual performance lead to a swamping of working memory that temporarily reduces anxiety (Boyer and Liénard, 2008). Particularly, in ritual behavior, the attentional focus on low-level features of action (action parsing), requiring high cognitive control during performance, would have the effect of overloading working memory. Working-memory loading might make it more difficult for anxiety-inducing thoughts to become conscious (Boyer and Lienard, 2008). In this view, ritualized behavior may constitute a spontaneous and efficient form of thought-suppression process (Wegner, 1994).

Even though motor performance and cognitive load seldom appear separated from each other, from an evolutionary perspective, rituals primarily appears as a motor phenomenon, as demonstrated by the finding that repetitive physical action (rather than cognitive demands) is mostly responsible for reducing physiological arousal due to anxiety-related unpredictability [42]. The sensorimotor experience of engaging in sequenced actions that are rigid, formal and repetitive, coupled with the motor control required to enact these actions, per se satisfies a fundamental need for order and control.

3.3 Social function

In nature, the most complex and elaborate forms of ritualization concern social rituals, where the repetition and magnification of ordinary acts acquire a communicative value. In ethology, ordinary or physiological acts (e.g. FAPs) are removed from their original and pragmatic context and “exapted” into a signalling function (Immelmann and Beer, 1989). Non-ritualized behavioural patterns can also function to communicate information (e.g., shivering or piloerection may convey information about the likelihood of flight or fight responses). However, ritualized behaviour has been specifically selected for its communicative effect, regardless of whether the original motor pattern served for communication or not. The repetition of ordinary acts, typically in an exaggerated and magnified form, makes the communicative signal precise, clear and less ambiguous, i.e. species-specific (Bekoff and Allen, 1995). The result is the simplification of communication, i.e. the overt manifestation of intentions that is accomplished through rituals. Across phylogeny, ritual behaviour reduces the cost of communication by transmitting honest signals of fitness or dispositions (Bradbury and Vehrencamp, 2000; Gintis et al., 2001). In this respect, sexual and social selection play an important role in the evolution of intraspecific (intrasexual and/or intersexual) ritualized behaviors. The redundancy and the exaggeration of ordinary acts may be selected and magnified by female choice (intersexual selection), as well as by competition over mates and resources (intrasexual selection) (Tonna et al., 2019).

Interestingly, according to the signal-detection theory to animal communication (Wiley, 1994), the evolution of exaggerated communicative signals may have been an adaptive response to a low-responsiveness to signals due to an “Error management” (i.e. a bias to under-valued signals as a consequence of uncertainty in correctly discriminating signals) (Johnson et al., 2013). A relevant example is represented by the evolution of the so-called pecking courtship behavior in gallinaceous birds as exaptation from feeding behaviour. The ritualization of the movement of pecking into a courtship behavior might have evolved through female choice, originally attracted by the possible presence of food (intersexual selection) (Stokes and Warrington Williams, 1971).

Intra-specific communication is inextricably tied with group cohesion: social rituals promote motor synchronization that is the basis of intra-specific communicative connection (Tonna et al., 2019). Behavioral synchronization is well documented in both vertebrates and invertebrates, from multicellular organisms (Placozoa) to humans. Rather, synchrony plays a role in almost every aspect of group behaviour. Namely, synchronized activity enhances 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)

The same adaptive significances suggested for animal rituals (e.g. intra-specific communication and group cohesion) have been described for human collective rituals. As in animal behavior, the uncertainty to discriminate the correct signal in social contexts (Johnson et al., 2013) lead to the development of communicative “hyper-signals”. Cultural rituals convey precise, unambiguous forms of communication, through the simplification and magnification of the communicative signal. In this way, they contribute to regulate hierarchy levels, social relationships and life-stages transitions. An example is represented by the rites of passage, where a clear, ostentatious demarcation occurs from a pre-existing state into a liminal status prior to the reincorporation into a new social category (Van Gennep, 1908). Similarly, entrance into “special” social classes (e.g.

shamanic practitioners) is rigidly restricted by ritualistic initiations (Singh, 2018). Whenever a transition occurs from one "coordination equilibrium" to another (Lewis, 1969; Dalkiran et al., 2012) or a passage to a different social class, ritual behavior intervenes with high-communicative and unmistakable signals of the happened transition or individual transformation. Therefore, on the one hand, human rituals appear as clear demonstrations of commitment in human societies (Kuran, 1998; Gintis et al., 2001; Sosis, 2003). On the other, ritual coordination facilitates the circulation and renovation of symbolic representations and mythological systems of the group (Eliade, 1948; Durkheim, 1963), and thus the consolidation of the "sacred values" of community (Ginges et. al., 2007). In this connection, ritual behavior represents the social "space" in which a common knowledge is created and the coordination of the group is reinforced (Chwe, 2001). Thus, the communicative function cannot be uncoupled from ritual effect of enhancing cooperation, shared intentionality (Reddish et al., 2013) and therefore group-cohesion (Sosis, 2000).

At a deeper level, ritual motor synchronization is a vehicle for intimate communicative and emotional bonding [60]. In different cultural rituals (such as initiation rites, preconflict rituals, religious rituals showing devotion) a deep emotional and "spiritual" cohesion is linked to harmful or "traumatic" ritual activities, such as beating, scarring or self-mutilation (defined as "high-arousal" rituals) (Whitehouse, 2004; Atkinson and Whitehouse, 2011). These coordinated and "traumatic" practices promote group cohesion and pro-group actions through the creation of identity fusion among individuals (Kavanagh et al., 2018). Moreover, the deliberately bloody and stressful ritual acts further increase collective memory retention and so reinforce cultural meanings (Connerton, 1989). Noteworthy, the smaller the average community size, the more rituals tend to manifest through traumatic activities (Jones, 2013). This is in accordance with the finding that bloody or hazing activities are able to reduce newcomers' ability to free ride around group entry and therefore to strengthen initiations into high-trust coalitions (Cimino, 2011).

Motor synchronization and high-arousal activities cooperate to create intensely committed groups probably via complex neuro-endocrine cascades. For instance, the repetitive and often strenuous actions of rituals stimulate the endocannabinoid system (Xygalatas, 2008) and the increase of endorphin production (Tarr et al. 2016) potentially resulting in anxiolytic and bonding effects. Moreover, synchronized motor actions activate oxytocin system. Oxytocin-related peptides show a strikingly molecular and functional conservation in behaviour from roundworms to humans, playing a critical role in reproductive behaviour and other biological functions (such as learning and memory, food arousal, and predator/prey relationship) (Lockard et al., 2017). In humans, oxytocin maintains its central role in affiliative and prosocial interactions (Ross and Young, 2009) and would be critically implied in the emergence of spiritual-like beliefs (i.e. the belief in a meaningful life pervaded by a sense of connection to a Higher Power, the world or both) within groups (van Cappellen et al., 2016).

We want to emphasize that ecological and social rituals are two sides of a unitary phenomenon, at work respectively in non-social and social contexts. The underlying mechanism is the non-functional and non-automatic repetition of FAPs or habitual ordinary acts, displaced from their original purpose, to make the environments (non-social or social) more predictable and ordered. It follows that the homeostatic function (ultimate causes) of ritual behavior on ecological and social systems is based on the same formal features (proximal mechanisms), thus representing a unitary process. In natural environments, ritualized action guarantees the necessary flexibility in order to regulate a fine “attunement” between changing environments and behavioural adjustments. Similarly, in social contexts, intraspecific selection promoted identical proximate mechanisms to control social unpredictability: the precise intra-specific signalling of action sequences guarantees a fine communicative “attunement” between conspecifics as well as regulates social relationships within the group. At the same time, synchronized physical action promotes intra-group connection with a stabilizing and predictability effect on social organizations.

4. Psychopathology of ritual behavior

Many psychopathological conditions may arise from failure or dysregulation of evolutionarily conserved functional systems (Nesse and Stein, 2012). In this connection, psychopathology of ritual behavior may throw light on the evolutionary significance of adaptive functions of the corresponding normal behaviour. An evolutionary framework of psychopathological compulsions is intriguing since ethological and psychopathological studies have repeatedly 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). Even though psychopathological compulsions and cultural rituals are both inherently compelling, psychopathological compulsions differ from collective rituals since their "private" character; that is, OCD compulsions are alienated from the social milieu and generally constructed as egodystonic, whereas cultural rituals are socially approved and collectively performed (Dulaney and Fiske, 1994; Lienard and Boyer, 2006).

Recent studies confirm a dimensional architecture of OCD (Barahona-Correa 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).

Actually, rituals would represent a normal behavioural repertoire in human development (infancy and childhood). This developmental phase is characterized by perfectionism, preoccupation with ordering objects "just-so", attachment to a favourite object, concerns about dirt and cleanliness, preferred household routines, actions repeated over and over or a specific number of times, rituals for eating, awareness of minute details in the home, hoarding, and bedtime rituals. Consistently, childhood rituals have been conceived as a mechanism for organizing, accommodating to and eventually mastering the environment (Langen et al., 2011). Moreover, ritual behavior maintains a crucial role in such critical life-stages (pregnancy, motherhood) where the control on the environment exerts a particular evolutionary significance (Boyer and Liénard, 2006). Noteworthy, childhood and life-stages rituals appear indistinguishable in both formal features and contents from pathological compulsions [10] and do not differ across the cultural groups (Zohar and Felz, 2001), thus suggesting underlying innate, pre-programmed motor patterns of behavior (Rapoport et al., 1994).

Ritual compulsions tend to exacerbate into a full-blow obsessive-compulsive disorder (OCD) if preceded by childhood traumatic experiences (both emotional abuse and neglect) which disrupt normal neurodevelopment. The strong association between childhood trauma and the later onset of obsessive-compulsive symptoms (OCS) or disorder (OCD) has been replicated in different studies (de Silva and Marks, 1999; Mathews et al., 2008; Briggs and Price, 2009; Miller and Brock, 2017). Interestingly, the same motor and cognitive mechanisms underpinning ritual behavior in humans have been invoked to explain the association between OCD and trauma. Particularly, it has been hypothesized that compulsive behavior would serve as a means to escape the intrusive-trauma-related negative emotions and anxiety (Miller and Brock, 2017); that is as an adjustment mechanism directed to a trauma-induced "high-entropy" state. The hyper-attention to the motor acts (especially, the smaller units of the action-flow) (Legare and Souza, 2012; Hobson et al., 2018), coupled with an overloading of working memory (Boyer and Liénard, 2006), concur to regain predictability to a psycho-social environment.

Nevertheless, it is in psychopathology where the ultimate causations of rituals mostly manifest, even though in a distorted form. In this respect, psychopathology may represent a favoured viewpoint from which to investigate ritual phenomenon since its shared biological and cultural underpinnings. The phenomenological "core" of OCD lies in a pervasive, pathological feeling of disorder (*aneidos*) (von Gebsattel, 1938), i.e. the perception of a constant high-entropy condition which may be subjectively expressed in spatial (symmetry obsessions), organic (contamination or hypochondriac obsessions) or moral (sexual and religious obsessions or aggressive compulsions) terms. Consistently, it has been hypothesized in OCD patients a specific impairment in safety signalling (mediated by vmPFC circuits) that would undermine the right estimation of environmental threat and unpredictability (Milad et al., 2013; Apergis-Schoute et al., 2017). The inability to update threat evaluation and an overestimation of environmental unpredictability would generate a permanent feeling of uncertainty and disorder, which in turn “triggers” the recourse of ritual compulsions. In this connection, OCD compulsions may be conceived as the hyper-expression of a normal, highly evolutionarily conserved “protective response” (Rapoport et al., 1994; Nesse and Stein, 2012) that functions as a behavioural copying strategy in a changing and unpredictable environment.

Since the extensive connectivity between prefrontal and basal ganglia structures in humans, OCS occur in different neurodevelopmental disorders, such as autism spectrum disorders or attention deficit hyperactivity disorder (ADHD) (Brem et al., 2014). Moreover, compulsions frequently are present in neuropsychiatric syndromes (Tourette's syndrome, post-encephalitic Parkinson’s disease, mental retardation, dementia) (Turbott, 1997).

OCD also represents a frequent synchronic (Tonna et al., 2015) or diachronic (Cederlöf et al., 2015) comorbid condition in major psychoses (schizophrenia and bipolar disorder), both of them implying specific prefrontal impairment with cortical-striatal dysconnectivity (Lewis et al., 2004; Ekman et al., 2010). 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).

Interestingly, in attenuated forms of schizophrenia (particularly in low-level disorganization psychoses) mild OCS appear to mitigate functional decline, inherent to schizophrenic process. 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. Once again, the mechanism at work would lie in an ordering and stabilizing effect of OCS, covering psychotic disorganization (Tonna et al., 2016b; Tonna et al., 2016c).

Altogether, OCD psychopathology reveals a strong association between the recourse of ritual compulsions (based on individual predispositions) and the function of regaining order and control over unpredictability states, inherent to OCD phenomenology or due to comorbid biological (e.g. psychotic vulnerability) or psychosocial (e.g. trauma exposure) conditions.

5. Ritual behavior and symbolic thought

The search of a possible continuity of ritual behavior from animals to humans cannot ignore the fact that rituals in human cultures are invariably symbolic activities (Penner, 1992). Therefore, one may question if an unbridgeable gap (in terms of proximate and ultimate causes) divides animal ritual behaviour from such complex symbolic manifestations, which are central to every human culture (Turner, 1985; Staal, 1989)

Regardless to the variegate manifestations and the different occasions for ritual performance (propitiatory or apotropaic, therapeutic or initiation rituals, seasonal rites - Lehmann and Myers, 1993-), exactly like animal ritual behavior, in every human culture, ritual behavior is 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) to be transformed into symbolic expressions (Turner, 1971; Penner, 1992).Interestingly, the perceived efficacy of rituals increases with the familiarity to the symbolic framework of the ritual performance (Anastasi and Newberg, 2008); in turn, the symbolic meaning is reinforced each time rituals are executed (van Gennep, 1909).

The acquisition of a symbolic conscience is linked to the cultural explosion (often referred to as a “big bang”), which happened after 60,000 years ago, during the Middle/Upper Paleolithic transition. Probably, there was no a single “big bang” , as a whole series of cultural sparks, occurred in slighty different times in different parts of the world between 60,000 and 30,000 years ago (Mithen, 1996; Renfrew, 2007).

To think symbolically implies the ability to deconstruct our exterior and interior worlds into vocabularies of discrete mental symbols that can be rearranged to produce alternate perspectives and to envision new possibilities, even about the unobservable (Tattersall, 2016).

The rise of symbolic thought dramatically changed the way we perceive the world, the others and ourselves [105]. Such symbolic matrix is so pervasive that humans have become “biologically” dependent on symbolic culture during ontogeny. Indeed, almost every aspect of human “biology” (including the plasticity of human brain) is epigenetically shaped by symbolic culture (Tylor, 1871; Kroeber, 1952; Deacon, 2000; Heyes, 2003).

5.1 Symbolic ecologies

We suggest that the “emergence” of symbolic activity dramatically widened the concept of environmental unpredictability. In fact, symbolic thought promoted a detachment from a pre-reflective, immediate and embodied adherence to reality to a reflective, symbolic-mediated contact. Through symbolic thought, humans acquired the unique property to dissect and recombine their animate and inanimate surroundings into a mass of intangible symbols to the point to inhabit partly in worlds of symbolic self-creation, which ended to “complete” every aspect of reality [86][87][88][89]. We speculate that by amplifying anxiety-provoking conditions of unpredictability, the emergence of a symbolic conscience enhanced the “urge” to ritualization. The mismatch between a novel “symbolic” environment and adaptive phenotypes represented the evolutionarily conserved cue for ritual behaviour, which in turn, was already suitable to give order to such a culture-mediated world, based on the biological predisposition of human brain to ritualization and its particular adaptive significance. Although the anthropological literature already highlighted such ecological function of ritual behavior (Malinowski, 1922; Wallace, 1966; Dulaney and Fiske, 1994, Fiske and Haslam, 1997), it did not provide any explanation of the possible underlying proximate mechanisms. We propose, on the basis of the analysis of ethological, psychobiological, psychopathological and anthropological data, that human and nonhuman “compulsion” to ritualize share the innate predisposition to perform repetitive motor patterns of actions in response to the challenge of environmental unpredictability.

Cultural rituals primarily fulfilled the function to redefine space and time in cultural terms (Cornford, 1912; Eliade, 1959; Durkheim, 1963; Dulaney and Fiske, 1994). In this respect, all the foundation rites share the function of cultural creation of a sacred central place from which to orientate spatio-temporal parameters and to regulate their connections to cosmic levels. Moreover, cultural rituals intervene with a homeostatic function to regulate the “right” course of natural (seasonal and cosmic cycles) and human events (individual life-stages) as well as to compensate any ecological “disordering” threats (Malinowski, 1922; Sosis and Handwerker, 2011). The invariance and constancy in formal structure of human ritual practices cannot be uniquely explained by cultural transmission, but underlie universal cognitive processes of the human mind (Levi-Straus, 1958; Dulaney and Fiske, 1996; Lienard and Boyer, 2006), whose proximal mechanisms are genetically fixed (as in other animals) and rooted in the specific motor action flow of ritual behavior.

5.2 Symbolic societies

The ecological and the social function of ritual behavior within unique human eco-cultural niches is undistinguishable, since their continuous and interdependent nature. With the emergence of symbolic thought, human communities became imbued with symbolic values, at the basis of the cohesion and identity of the group. Actually, human societies are held together by a cultural web of symbolic representations, which serve to generate and maintain meaning, extending biology in every aspect of human life (Geertz, 1973). Such symbolic webs of significance, distributed among individuals, have to be continually recreated by people through ritual ceremonies and practices. (Cohen, 1985). The consciousness of community has to be kept alive not only on face-to-face interactions between individuals but through concrete, bodily manipulation of its symbols. In this respect, ritual behavior gives the unique possibility to encode and reinforce symbolic values through concrete bodily actions, coupled with the active incorporation of material culture; that is, to integrate embodied interactions and materiality (Connerton, 1989).

Within eco-cultural niches, cultural rituals may have had a pivotal role in gene-culture coevolution, mediating the intertwining of brains, bodies, things and symbols in the shaping and evolution of *Homo sapiens* as cultural animal (Renfrew, 2008; Hodder, 2011). Cognitive abilities and personhood emerge in interaction of brain and body with the material world (Hutchin, 2008); thus, rituals, providing the glue needed for social cohesion, may have represented the vehicle through which such complex bio-cultural feedbacks could be at work. The deep interconnection between rituals and symbolic activity brought to the creation of a systematic and ordered cultural world, symbolically rich but embedded in materiality, promoting the process of "culturing nature" (i.e. the transformation of wild into cultural), typical of our species (Hodder, 2001).

Consistently, ritual behavior appears to precede (and promote) the development of more complex religious systems in human cultures, such as the birth of "moralizing high gods" (Whitehouse et al., 2019), and other fundamental "tipping points" of human cultural evolution, for example the initial rise of complex societies and the appearance of agriculture (Cauvin, 2000; Schmidt, 2005). In this respect, we want to emphasize that ritual behavior may have been the medium of such long-term environmentally and culturally derived plastic changes in the functional architecture of our brain (Watkins, 2017).

6. Discussion

In the present contribution we referred to precise behaviourally criteria, starting from the notion of "ritualized behavior" (Rappaport, 1979; Liénard and Boyer, 2006). If rituals are conceived as a specific way of organizing the flow of action, an underlying highly conserved formal structure becomes evident from animals to humans with psychopathological compulsions at the crossing point. Not less strikingly is the invariance of themes, crossing different cultures (Dulaney and Fiske, 1996; Lienard and Boyer, 2006) and linking different disciplines (ethology, psychopathology and anthropology). Moreover, ritual behavior is a constant tendency of every culture (Turner, 1985), remarkably persistent through the history of mankind (Staal, 1989), going back to the earliest human groups and down to Neanderthals (Trinkaus et al., 1993; Mithen, 1996). Therefore, an evolutionary framework, able to explain ritual behavior in the light of its phylogenetic continuity is intriguing. Previous evolutionary models (Abed and de Pauw, 1998; Szechtman and Woody, 2004; Boyer and Lienard, 2006) have focused on supposed highly conserved systems of our brain: for example, a "security motivation system", evolved to handle the uncertainties of potential "disordering" threats (Szechtman and Woody, 2004; Woody and Szechtman, 2013) or a "Hazard-Precaution system", i.e. a specific safety-motivation system dealing with potential danger (Boyer and Lienard, 2006). All these models may contribute to explain the remarkable invariance and species-specificity of human ritual brain and give reason of some of the specific formal features of ritual behavior. Nevertheless, their descriptions are generally confined to the cognitive machinery underpinning ritual action, not investigating the proximate and ultimate causes of ritual behavior prior to the evolution of cognitive abilities. The result is to conceive human rituals as a "by-product of evolved cognitive architecture" (Lienard and Boyer, 2006) and to conceive animal rituals as "a case of behavioural analogy" (Boyer and Lienard, 2006). Our hypothesis is that ritual behavior primary developed as the exaptation of specific motor patterns, with evolutionarily conserved formal features (rigidity, formality and repetition) aimed at increasing environmental (ecological and social) stability under conditions of unpredictability. This model is not in contrast with previous evolutionary models but highlights the primordial motor foundation of ritual behaviour, as homologous phenomenon from animals (vertebrates and invertebrates) to humans. The focus to the motor architecture of ritual behavior (pre-cognitive and pre-symbolic) permits to connect directly the phylogenetic roots of human rituals to repetitive motor patterns of non-human animals, and therefore to grasp the striking evolutionary continuity (in proximate and ultimate causes) of ritual behavior from invertebrates to humans. Ethological and neurobiological data strongly support that the "urge" to motor repetition for ecological and social functions may be better explained as an example of evolutionary homology (rather than as a behavioural analogy). This homologous continuity is corroborated by psychopathology of OCD, intended as a magnified or distorted expression of a normal behaviour and its original function (Nesse and Stein, 2012). Even though previous models have stressed the importance of OCD compulsions in order to understand the evolutionary function of human rituals, it has not been sufficiently highlighted the high phylogenetic proximity of OCD compulsions with animal rituals, insisting on shared and evolutionarily conserved neural circuits, formal features and adaptive significances, which directly connect non-human and human rituals.

According to this model, even though human collective rituals appear inextricably embedded in symbolic significances, they remain irreducible and highly conserved motor displays (proximal causes or mechanism), with an inherited compulsory character (Rappaport, 1979; Tambiah, 1985), whose adaptive function, “triggered” by the same selective pressures, is to cope with ecological and social conditions of unpredictability (ultimate causes). The rise of symbolic activity in *Homo Sapiens* emphasized the drive to ritualization in human cultures to face the “emergent” problem of ordering a novel symbolic-mediated world. Even since then, ritual bodily actions became symbolic activities deeply imbued with myths, spiritual beliefs and religious experiences acted to reinforce the shared memory and the cultural identity of the groups. Nevertheless, ritual behavior remains for itself primarily a motor phenomenon, rooted in the biological constraints (genetics and epigenetics) of our species, thus, pre-symbolic, i.e. “pure activity, without meaning” (Staal, 1989). In other words, the “compulsive” motor pattern to repeat, typical of all rituals, is genetically inborn and not merely an effect of cognitive abilities. Built on this “fixed” motor structure, the evolution of cognitive and symbolic capacities have generated the complexity of human rituals.

Ethology of ritual and compulsive-like behaviour

1. Introduction

1.1 Ethology of ritual

1.1.1 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).

1.1.2 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 spatiotemporal 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 spatiotemporal 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).

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).

1.1.3 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). FAPs and 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 Lienard, 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).

1.2 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., 2012). 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).

1.3 Marble burying

Burying, burrowing, and digging form part of the normal behavioral repertoire of rodents, in both the wild and the laboratory. These species-specific behaviors are mostly aimed at searching for food, burying both noxious and harmless objects, and building adequate nurseries capable of protecting individuals against predators and providing suitable environments to breed. Burying and digging are expressed in relatively nonanxiogenic scenarios (e.g., nesting, hoarding, foraging), as well as under anxiogenic circumstances (e.g., burying of noxious objects, confronting predators). In the last case it is referred to as “defensive burying” (Wolmarans et al., 2016). “Defensive burying” was first described by Pinel and Treit (1978), with regard to the rodent behaviour of moving any available loose material toward various stimulus-objects in a seeming attempt at covering them.

“Neophobic burying” refers to an anxiety-related form of burying related to novelty-induced anxiety, following exposure to novel, but nonreactive and harmless objects (Torres-Lista et al., 2015). In theory, whereas animals demonstrate non-habituation toward defensive burying, neophobic burying should attenuate over time following repeated exposure to the same stimuli (Londei et al., 1998).

Defensive burying has been persistently used to test avoidance-dependent anxiety in a number of studies. Instead, the proposal of a ‘risk-assessment’ function of ‘neophobic burying’ (Pinel et al., 1994) admits a cognitive component in the function, but maintains the traditional, avoidance motivation. Nevertheless, an abundance of literature has demonstrated that rodents often persist in burying harmless forms of stimuli in the absence of anxiety—which is referred to as “inherent burying”, of which marble-burying (MB) is a typical example (Wolmarans et al., 2016). As such, it has been hypothesized that this represents non-functional repetitive behavior analogous to the behavioral symptoms of Obsessive–Compulsive Disorder. Namely, the occurrence of non-functional, OCD-like burying would be much more compatible with an investigative, than defensive function of burying (Londei et al., 1998).That is, MB might be better conceived as a compulsive-like behavior, derived from environmental investigative FAPs, causing anxiety and distress in rodents. Interestingly, anxiety often occurs as a consequence rather than a cause of OCD in humans. Moreover, the finding of no habituation in mice, burying non-reactive, stimulus-objects, further support the hypothesis of a relationship between the burying of glass marbles by laboratory rodents and OCD (Njung'e and Handley, 1991).

The present study was aimed at assessing the hypothesis that MB behavior may represent a compulsive-like behavior, built on pre-programmed rodents' investigative/explorative motor patterns over the environment. As such, we want to assess if MB behavior share those specific formal features (in terms of rigidity, repetition and duration) which characterize ritual behavior in non-human and human animals.

2. Methods

2.1 Sample

The animal model of compulsive-like behaviour was based on the ethological analysis of conditional knockout mice for NPY1R KO and wild type mice during a Marble Burying Test.

Neuropeptide Y (NPY) plays an important role in stress, anxiety, obesity, and energy homeostasis via activation of NPY-Y1 receptors (Y1Rs) in the brain. We adopted conditional knockout mice in which the inactivation of the Npy1r gene was restricted to excitatory neurons of the forebrain, starting from juvenile stages (Npy1rrfb). Npy1rrfb mice exhibit increased anxiety and reduced body weight, less adipose tissue, and lower serum leptin levels (Bertocchi et al, 2011).

The ethological analysis was conducted based on records from a previous study conducted in the Department of Chemistry, Life Sciences and Environmental Sustainaibility, Unit of Behavioral Biology of the University of Parma.

In order to dissect a confounding role of anxiety, both NPY1R knockout and wild type mice had been previously assessed through the “Elevated Plus Maze” and the “Open Field” tests.

2.2 Instruments

2.2.1 Ethogram

A species ethogram is a complete list of species-specific behaviors, describing the elements and function of each behavior performed by the animal. Behaviors in the species ethogram may be combined, excluded, or emphasized in the design of ethograms used for particular research questions (such as assaying aggressive behavior, or abnormal behaviour like compulsive behaviour).

The ethological observation has been focused on the following active behaviors:

- Undirected sniffing: a general investigatory behavior which is not directed to a specific object in the environment. It serves to locate or detect olfactory stimuli, to investigate the local microenvironment, or to investigate the macroenvironment (outside of the cage).

- Directed Sniffing: such investigatory behaviour is specifically directed to a “novel” object in the environment (e.g. marble).

- Rearing: a variant of the search phase of exploratory behavior, when the animal is moving around the environment attempting to contact relevant stimuli. Rearing may be interrupted by brief bouts of attend or investigate behaviors when the animal encounters a stimulus. The animal will then return to general locomotion, or move to the next step in the exploration behavior chain (i.e. attend, approach or investigate as appropriate). Rearing serves to provide head elevation to attend or investigate more distant stimuli. As mouse vision is very limited, rearing is typically accompanied with the investigate - undirected sniffing variant of investigation.

- Grooming: it is an maintenance behavior which functions to maintain the physiological stasis, comfort, and appearance of the mouse. Grooming occurs sporadically during periods of activity and can become more intense after feeding.

- Digging: a form of nesting behavior which typically occurs at the beginning of the nesting behavioral sequence and involves the removal of substrate material from a certain spot. In wild mouse populations, digging can be observed while the mouse is searching for food or for the purposes of burrowing.

Such registered behaviors may be expression of environmental investigation/exploration (rearing, sniffing) or exploration of a “novel” object (e.g. the marble) (directed sniffing, manipulation). According to previous studies (Londei et al., 1998), grooming was considered as a possible expression of compulsive-like behaviour, as an alternative to MB.

2.2.2 Elevated Plus Maze

The elevated plus maze (EPM) is a test measuring anxiety in laboratory animals that usually uses rodents as a screening test for putative anxiolytic or anxiogenic compounds and as a general research tool in neurobiological anxiety research. The model is based on the test animal's aversion to open spaces. In the EPM, anxiety is expressed by the animal spending more time in the enclosed arms. Anxiolytic drugs specifically increase, and anxiogenic drugs specifically decrease, the number of entries into the open arms and the time spent there. The total entries score and total distance are considered a useful index of general activity. Total entries score is also an index of anxiety, and the percentages of entries and time spent in each arm constitute the index of primary anxiety. The open and closed arms are considered to evoke the same exploratory drive; therefore avoidance of the open arms is considered to be a result of the induction of higher levels of fear. It is thought that the aversion of mice to explore the open arms of the maze is caused by fear of open and elevated spaces (Rodgers and Dalvi, 1997).

2.2.3 Open Field

The open field is a very popular animal model of anxiety-like behaviour. The procedure consists of subjecting an animal, usually a rodent, to an unknown environment from which escape is prevented by surrounding walls. The procedure generally involves forced confrontation of a rodent with the situation. The animal is placed in the centre or close to the walls of the apparatus and the following behavioral items are recorded for a period ranging from 2 to 20 min (usually 5 min): horizontal locomotion (number of crossings of the lines marked on the floor), frequency of rearing or leaning (sometimes termed vertical activity), grooming (protracted washing of the coat). In such a situation, rodents spontaneously prefer the periphery of the apparatus to activity in the central parts of the open field. Indeed, mice and rats walk close to the walls, a behaviour called thigmotaxis. Increase of time spent in the central part as well as of the ratio central/total locomotion or decrease of the latency to enter the central part are indications of anxiolysis. Some authors use a procedure in which the animals are allowed free access to the open field, from a familiar cage (Prut and Belzung, 2003). In this case, the number of risk assessment postures directed to the open field may provide a good measure of the approach response toward novelty, that is, exploration.

2.3 Procedures

One week before the onset of our behavioral assessments, each animal was allocated individually to an automatic climate-controlled laboratory cage [42 (l) × 26 (w) × 15 (h) cm; Techniplast S.P.A., Varese, Italy] and maintained at 23 °C on a 12-h light/dark cycle (lights on at06 h00 and off at 18 h00). Food and water were provided ad lib for the duration of the study. The cages were cleaned and new bedding material was added weekly.

Animals were habituated in these cages in the absence of marbles for at least 24 h before the first MB test. To assess MB but prevent avoidance behavior,12 glass marbles (ø 1 cm) were evenly spaced on sawdust (the average flake size was 4 mm, in a layer 5 cm thick) in exact copies of the home cages. The 12 marbles were positioned at regular distances and in four rows. Each mouse was allocated to a marble-containing cage and allowed 30 min to explore. After returning the animals to their home cages, the marbles were counted. A marble was considered buried when 2/3 or more of its size was covered with sawdust. MB was measured in the same animals at intervals of 2 minutes. An elevated number of buried marbles may be considered index of compulsive-like behaviour.

Finally, an ethological analysis of the registered videos of the MB was conducted using the software "The Observer XT" (Noldus, Olanda), which allows to register specific parameters for each behaviour: frequency (total number), total duration) and latency. Every behavioural pattern has been assessed taking into account the specific position of the animal in the cage (periphery and centre).

2.4 Statistical Analysis

T test was used to investigate any differences in behavioural patterns between KO and WT populations during MB test.

Pearson's correlations (two tailed) were used to investigate the relationship among compulsive-like behaviour (grooming and MB) and behaviors of exploration of the environment (rearing, sniffing) as well as of the marble (directed sniffing, manipulation).

Three- way ANOVA was adopted to investigate the interactions between the following variables: sex x genotype x interval with regard to MB behavior.

Two-way ANOVA was adopted to assess the interactions between sex x genotype with regard to explorative behaviors (sniffing and rearing).

All statistical analyses were performed with SPSS for Windows (version 23.0; SPSS Inc, Chicago, IL).

3. Results

3.1 Study sample

The study sample was constituted by 11 NPY1R KO (8 male) and 15 WT (10 male) (Table 1).

	Knock-out	*Wild Type*
Male	**8**	**10**
Female	**3**	**5**

Table 1: Study sample

No differences were found between KO and WT in behavioural activity. Moreover, both KO and WT populations did no exhibit anxious behaviour in both *Elevated plus maze* and *Open field tests*. Therefore, we chose to apply the ethological analysis to the whole population (KO + WT) in the MB test.

3.2 MB, grooming and explorative behaviors

The correlations between compulsive-like behaviours (MB and grooming) and explorative behaviors are depicted in Table 2.

First, an inverse correlation was found between MB and grooming in both repetition and duration.

A direct association resulted between MB and sniffing (both repetition and duration), whereas an inverse association was found between perimetric digging (not directed to the marble) and perimetric sniffing. Finally, grooming was inversely related to MB and rearing and directly associated with sniffing (central and perimetric).

3.3 Sex differences in MB behavior

A significant difference was found between males and females (in both KO and WT) with regard to MB. Particularly, females buried a major number of marbles, with a minor latency, with respect to males. KO females buried a major number of marbles with respect to WT females (Figure 1).With regard to explorative behaviors, males were found to have higher perimetral sniffing behaviors as well as higher central rearing behaviors compared to females (Figure 2-3).

Behavior		**Ripetition (R)**			**Duration (D)**		
		Total (T)	*Center (C)*	*Perimeter (P)*	*Total (T)*	*Center (C)*	*Perimeter (C)*
Uncovered Marbles	Sniffing	-	-	.554**	-	-	.436*
	Marble	-.463*	-	-.586*	-.629**	-	-.680**
Marble *(D)*	Grooming	-	-	-.389*	-	-	-
Marble *(R)*	Grooming	-.457*	-	-.547**	-	-	-.404*
	Sniffing	-	-	-	-	-	-.519**
Perimetric Digging *(R)*	Grooming	-	-	-.405*	-.436*	-	-.444*
	Sniffing	-	-	-.473*	-	-	-.597**
Central Marble *(D)*	Grooming	-	-	-.510**	-	-	-
	Sniffing	-	.507**		-	.504**	-
Central Marble *(R)*	Grooming	-	-	-.512**	-	-	-
	Sniffing	-	.414*	-	-	-	-
Grooming *(D)*	Sniffing	-	-	-	-	-	.542**
	Marble	-	-	-.503**	-	-	-.501**
	Rearing	-.593**	-.468*	-.538**	-.574**	-.545**	-.465*
Grooming *(R)*	Sniffing	-	-	-	-	-	.399*
	Marble	-.457*	-	-	-	-	-
	Rearing	-	-	-	-.432*	-	-.389*
Perimetric Grooming *(D)*	Sniffing	-	-	-	-	-	.539**
	Marble	-.404*	-	-	-	-	-
	Rearing	-.504**	-	-	-	-	-
Perimetric Grooming *(R)*	Sniffing	-	-	-	-	-	.454*
	Sniffing Ball	-	-	-	-	-	.394*
Central Grooming *(D)*	Grooming	-	-	-.411*	-	-	-
	Sniffing	-	.721**	-	.491*	.792**	-
	Rearing	-	-	-.437*	-	-	-.445*
Central Grooming *(R)*	Sniffing	.394*	.729**	-	.458*	.771**	-
	Sniffing Ball	-	.400*	-	-	-	-
	Rearing	-	-	-	-.466*	-	-.551**

Table 2: correlations between MB behaviour, grooming and explorative patterns.

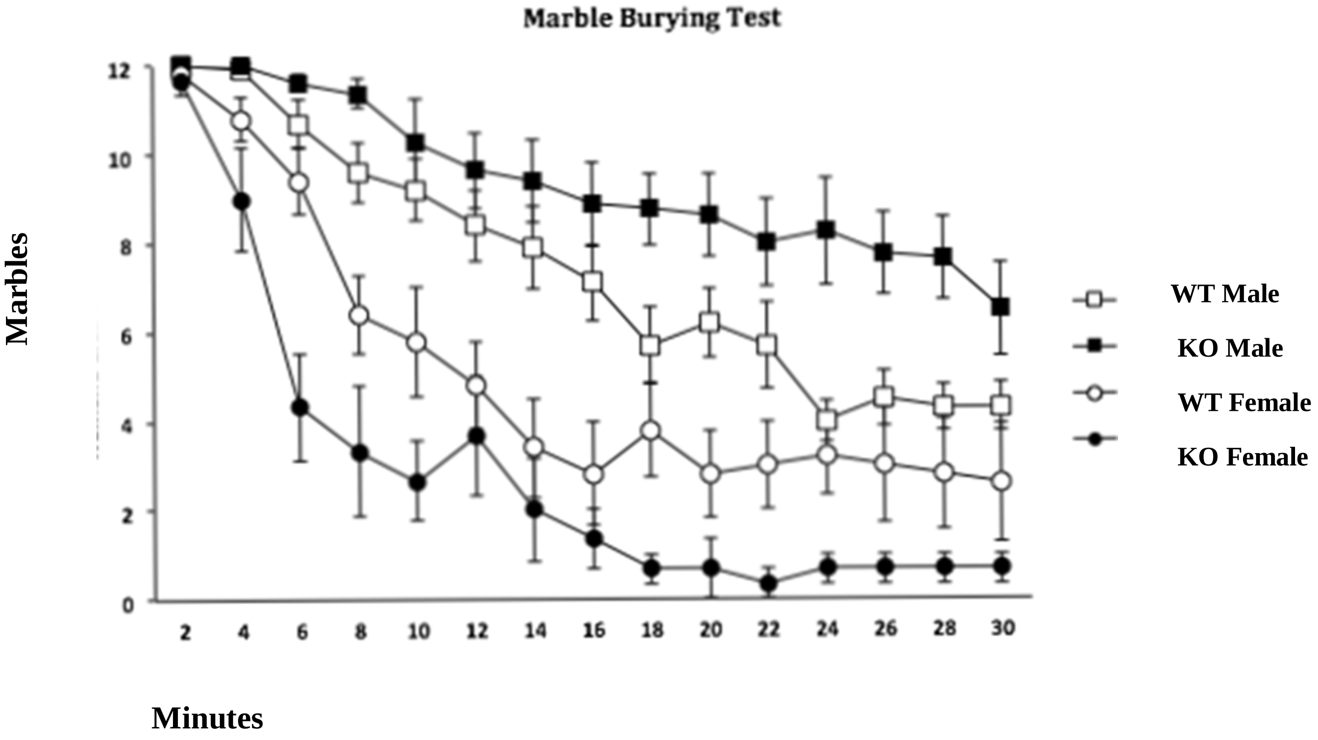

Fig.1: N° of unburied marbles / 2 minutes intervals

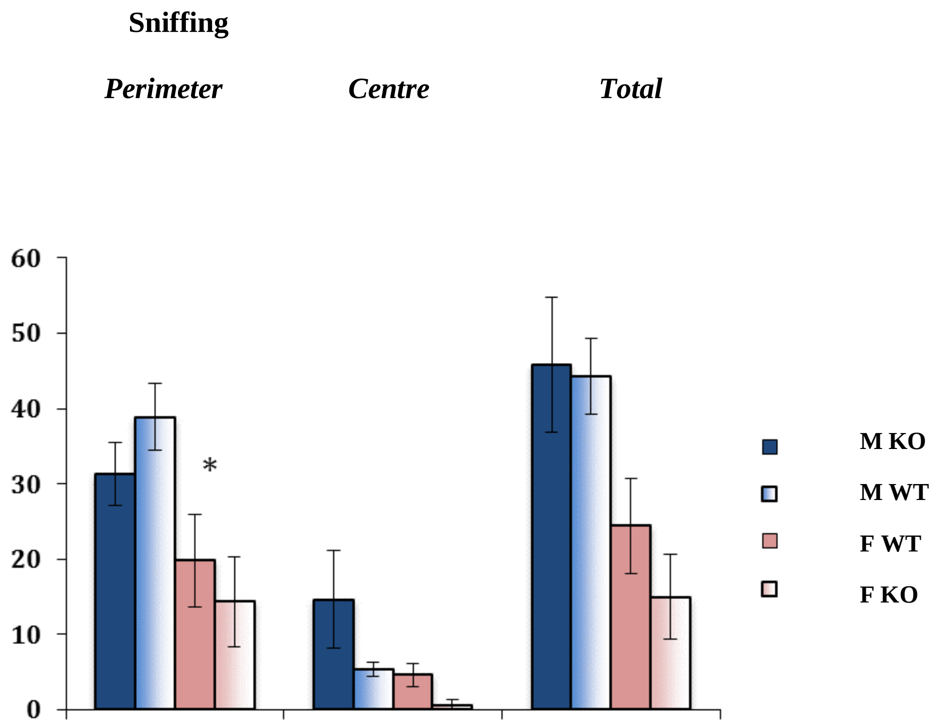

Fig. 2: Frequency of sniffing

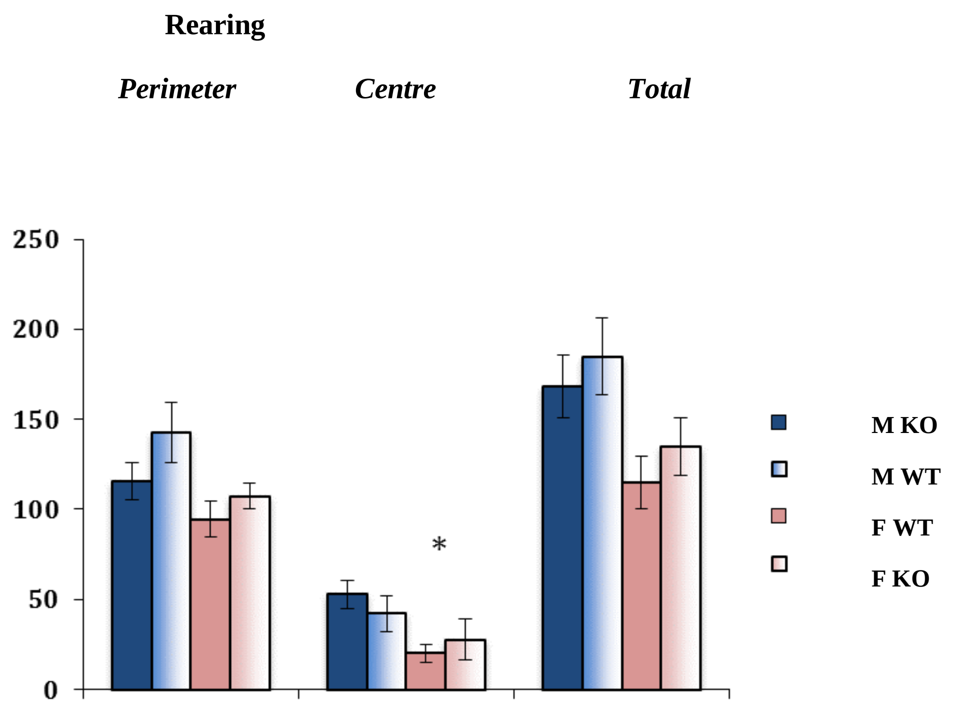

Fig.3 Frequency of rearing

4. Discussion

The present study was aimed to test the hypothesis that MB may be viewed as a compulsive-like behaviour based on pre-programmed exploratory/investigative FAPs. Our experiment was based on the assumption that related behavioural patterns (for example investigation patterns) correlate between each other over the variation of the situations and/or subjects (Londei et al., 1998). Our prediction is that in compulsive-like behaviors, MB is associated to a non-functional inflation (in duration and repetition) of a broader spectrum of explorative behavioural patterns.

Our findings seem to corroborate this hypothesis. Namely, an association was found between MB behaviour and sniffing; that is, the more mice are engaged in compulsive-like behaviour, the more they increase other exploratory behaviors, in both duration and repetition.

The consistently positive correlation found between a measure of exploration, that is sniffing, and MB activity, shows that both females and male mice performed burying proportionally to the subject's tendency to explore. This is consistent with previous results (Londei et al., 1998) and confirms the hypothesis that burying is motivated by investigation/ exploration of the environment, which does not exclude any defensive effect of this behaviour, yet. By contrast, in our study. perimetric digging inversely correlates to perimetric sniffing, thus suggesting that when digging is not directed to MB activity, it represents an alternative form of exploratory behavior. Therefore, the rodent appears more attracted than repelled by the stimulus-object it will bury, in evident contrast with previous models of MB activity as an index of avoidance-dependent anxiety. Moreover, MB did not result associated to other exploratory activities directed to the marble (e.g. marble sniffing, nose poking), indicating that MB cannot be interpreted as a neophobic behavior.

In our experiment, we found no habituation in MB over trials, in agreement with previous research (Njung'e and Handley, 1991), which demonstrated that prehousing with marbles did not reduce the number of marbles buried in the experimental cage. This further corroborates the model of MB as a compulsive-like activity partly uncoupled from neophobic motivation.

In the present study, a purely negative correlation was found between burying and self-grooming. This finding, confirming previous data (Londei et al., 1998), suggests that MB and self-grooming represent two alternative outlets of the same, in part non-functional, motivation. This result is in line with the experimental evidence of self-grooming as a compulsive-like behavior, even ending in self-injury, after frustration in restrictive environment. (Dallaire, 1993).

Finally, the increased duration of compulsive-like activity (besides its internal repetition) would suggest a cognitive component of behavior, a “just-like” perception of the act, typical of OC spectrum.

Overall, we found a significant sex difference in MB activity. Namely, females (both KO and WT) were more engaged in MB behaviour with respect to males: that is, females buried a higher number of marbles after a 30 minutes test and started to bury with a minor latency. KO females exhibited the highest levels of MB activity. We speculate that females may be more exposed to unpredictability-related anxiety (which, we suppose may be an evolutionary cue for compulsive-like behavior) since /investigative explorative behaviour patterns are less “fixed” with respect to males. In other words, in males a strictly pre-programmed repertoire of FAPs is automatically and more easily recruited to face environmental uncertainty compared to females.

Altogether, our findings would confirm the ethological model of compulsive behavior as inappropriate release of FAPs (Rapoport et al., 1988). Particularly, rodent burying behavior may be seen as the abnormal release of environmental investigative/explorative FAPs, whose non-functional inflation (in duration and repetition) would be produced by a subject having internal difficulty in finding alternative patterns when behavior does not attain its aims. Simply unusual external stimuli would be sufficient to maintain investigative compulsive-like behavior. The extension of non-functional repetition to a broader range of activity patterns (such as sniffing) suggests the inclusion of MB in exploratory behavioral patterns. Moreover, this finding would corroborate from an ethological viewpoint the conservative formal structure of compulsive rituals, based on non-functional repetition and longer duration of FAPs, detached from their original pragmatic goal. In other words, in compulsive rodents, ritualization tend to parasitize other explorative behavioral patterns, affecting their functionality.

Also the role of sex in this process (with the suggestion of a more difficult alternation of behaviours in females) would be an intriguing issue, which might lead to understanding the effect of sex on basic brain mechanisms.

Formal structure of psychopathological rituals

1. Introduction

In psychopathology, rituals of OCD are described as compulsions. According to the current diagnostic systems (DSM-5) (APA, 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-Correa 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).

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 Lienard, 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).

In the present study, we approached OCD behavior from an ethological perspective, which examines formal features of behavior on the basis of observations made by the experimenter. Following a model of human ethology to study motor rituals in OCD patients (Eilam et al., 2006; Zor et al., 2007), we videotaped OCD rituals performed by patients in their own home, and compared these rituals with the behavior of healthy individuals instructed to perform the same physiological act underpinning the ritual behavior. The videotaped rituals were deconstructed into their single “action units” performed at each location ⁄object (ritual basic components).

The study of ritual compulsions through an ethological analysis may represent a promising field of investigation since both ethological and psychopathological studies have repeatedly highlighted the striking similarities between animal habitual behavior and both human normal behaviors and pathological compulsions (Lorenz, 1966; Insel, 1988; Eilam, 2015). Moreover, an ethological perspective on OCD emphasize the study of specific formal characteristics of ritual compulsions, which has been partially neglected in favour of the investigation of the contents of obsessions and/or compulsions. Finally, no study to date investigated whether the formal structure of OCD compulsions might vary according to psychopathological variables of OCD (e.g. severity and level of insight) or other comorbid psychopathological dimensions (e.g. depressive symptoms). Not even explored is the relationship between formal features of compulsions and premorbid personality or other trait conditions, such as psychotic vulnerability. This may be an important issue, since the complex interaction between OC and psychotic dimensions in schizophrenia spectrum (Tonna et al., 2015). Similarly, despite the high association between childhood trauma (both neglect and abuse) and later onset of OCD, a possible effect of traumatic experiences on the formal structure of OCD compulsions has never been investigated.

Therefore, the present study was aimed at evaluating through an ethological approach: 1) the specific formal structure of ritual compulsions compared to that of the corresponding ordinary behaviour of healthy controls; 2) whether formal features of OCD compulsions may be conditioned by psychopathological variables, trait conditions (personality and vulnerability to psychosis) or by childhood traumatic experiences.

2. Methods

2.1 Participants

OCD patients: All participants were recruited from the Psychiatric Unit of the University Hospital of Parma from July 2017 to July 2019. Patients were included in the study if 1) they were aged older than 17 years; 2) they received a diagnosis of Obsessive-Compulsive Disorder (OCD), according to DSM-IV criteria (American Psychiatric Association, 2000); 3) a written informed consent to study participation was obtained. Patients were excluded if they were affected by 1) a current mental disorder related to a general medical condition or to a drug or alcohol abuse or dependence; and 2) a cognitive disorder (Mini-Mental State Examination score lower than 25), which could impair the compliance with testing procedures.

Control individuals: A matched healthy individual of similar age and gender was asked to perform the same task that formed the OCD ritual. For example, if a patient described his/her ritual as “lighting a cigarette”, the respective control was requested to “light a cigarette”.

2.2 Instruments

The Structured Clinical Interview for DSM-IV (SCID-I) (Mazzi et al., 2000) confirmed the diagnosis of Obsessive-Compulsive Disorder. All subjects competed the Structured Interview for DSM-IV Personality Disorders (SIDP-IV) (Pfhol et al., 1995) for the assessment of personality traits. The severity of OCS was measured with the Yale-Brown Obsessive-Compulsive Scale (YBOCS) (Goodman et al., 1989) while the severity of depression was assessed through the 17-items Hamilton Rating Scale for Depression (Ham-D) (Hamilton, 1960). Finally, the assessment of basic symptoms of schizophrenia was performed using the Frankfurter Beschwerde-Fragebogen (FBF) (Süllwold, 1986).

A trained psychiatrist interviewed patients after the resolution of the acute phase of illness to guarantee an adequate cooperation to the assessment.

2.3 Treatment

All patients were treated with a serotoninergic medication (SSRI or TCA). Patients resistant to serotoninergic drugs also received low-doses of high-potency antipsychotic medication in augmentation.

2.4 Procedure

After an accurate description of the research and the approval to participate, patients were asked to provide a videotape of their rituals. Videotape could be registered by the patient himself or by a relative. It was stipulated to the patient that he⁄she were requested to display recent and frequent rituals. When asked to rate the degree of similarity, patients reported a medium or higher degree of closeness of the videotaped ritual to their off-camera compulsion. Consistent with the patients high ratings, we noted that once patients started to perform their rituals, performance took over and they paid no further attention to the observer or the camera but only to performing the ritual itself.

2.5 Data acquisition and ethological analysis

A ritual was defined as the set of movements performed to accomplish a task as specified by the patient. The ritual included all the acts displayed within the task. The beginning and end of a ritual were determined by the patient’s activity.

Motor behavior was scored during playback of the video records. We listed the acts that comprised each ritual. Behavior was scored using "the Observer" (Noldus Information Technology, Wageningen, the Netherlands), a software for ethological descriptions.

Shared (functional) and unique (non-functional) acts: According to Zor and colleagues (2009), for each OCD patient and her/his matched control individual, we divided the acts in those performed by both individuals, and in acts that were performed by only the OCD patient or by only the matched control. Acts performed by both were classified as "shared", and were considered as being essential to the performance of the task (i.e. "functional"). Acts that were performed by only the OCD patient or by only the control individual were classified as "unique", and were considered as being not compulsory for the task (i.e. "non-functional"), as the other person skipped that act or used an alternative act. For each OCD ritual and matched control performance, the following parameters were extracted from the video files: ritual duration, incidence and duration of all acts, acts repertoire (number of different acts, excluding repetitions), incidence and mean duration of shared and unique acts, chain length of consecutive shared acts and chain length of consecutive unique acts, incidence of switching between shared and unique acts, frequency distribution of act durations.

2.6 Statistical analysis

T-test was adopted to compare OC rituals and corresponding behaviors of healthy controls.

Pearson's correlations (two tailed) were used to investigate the relationship among psychopathological variables, trauma and formal structure of compulsive rituals.

3. Results

3.1 Participants

Twenty-one OCD patients provided a videotape of their rituals. An equal number of healthy controls, matched for sex and age, were registered for corresponding physiological acts of OC rituals. Socio-demographic and clinical features of the sample of patients are depicted in Table 1.

3.2 Comparison between compulsive rituals and corresponding control behaviors

The comparison between psychopathological rituals and corresponding control behaviors are depicted in Table 2. Ritual behaviour differed from corresponding control behaviour with regard to the repetition and duration of functional acts; the number, repetition, duration and length of non-functional acts; the number of transitions from functional acts to non-functional acts and vice versa.

3.3 Psychopathological variables and formal structure of rituals

The correlations among psychopathological features and structure of rituals is reported in Table 3. No associations were found between psychopathological variables of OCD (BABS, YBOCS). With regard to personality traits, we found an association between Borderline and Histrionic traits and duration of functional and non-functional acts and between Obsessive-Compulsive traits and number of non-functional acts. A correlation was found between severity of depression (HAM-D) and duration of ritual behavior (total duration; number, duration and repetition of functional acts). Finally, a direct association was found between severity of basic symptoms (FBF) and the overall complexity of ritual (total number, duration and repetition of both functional and non-functional acts).

3.4 Childhood trauma and formal structure of rituals

The correlations between childhood trauma (CTQ total score) and formal features of ritual is reported in Table 4. Childhood trauma (CTQ total score) was associated with higher number of total acts, functional acts (FA) and non-functional acts (NFA), repetition of NFA and switches from FA to NFA.

4. Discussion

The present study was aimed at investigating the formal structure of compulsive rituals in OCD patients compared with analogous physiological acts of healthy controls. Second objective of the study was to assess whether the structure of compulsions might vary according to psychopathological variables, psychotic vulnerability and/or childhood trauma experiences. To our knowledge, this is the first study aimed at exploring the specific formal features of ritual compulsions also in relation to psychopathological of OCD or other comorbid conditions as well as to trait conditions. Particularly, the present study tested the hypothesis that the formal features of OCD compulsions might be conditioned by underlying psychopathology or by developmental adverse events (e.g. childhood trauma exposure) or vulnerabilities (e.g. psychotic) though maintaining a “fixed”, invariant structure.

First, our findings clearly indicate that compulsive rituals differ from physiological acts in many respects, corroborating the hypothesis that ritual behavior conserve a specific formal structure characterized by repetition of single action-units with inflation of non-necessary acts and diversion of the attention to the act itself (Zor et al., 2009; Eilam, 2015). Namely, in OCD, compulsions may be distinguished from corresponding physiological acts with respect to the following features. 1) Both functional (FA) and non-functional (NFA) acts were excessively repeated, thus confirming that compulsive rituals are built through the repetition of single action-units (both FA and NFA). 2) Duration of the act itself (regardless to whether they were functional or non-functional) was significantly longer compared to controls, thus suggesting a loss of automaticity with redirection of cognitive efforts to the “just right” of the acts or the “script” of the performance, with special focus on the smaller units of the action flow (*action parsing*). 3) There is a huge prevalence of NFA (in number, repetition, duration and length) with a complete detachment from a pragmatic goal (*goal demotion*). Moreover, the action flow is continuously interrupted by the more frequent transitions from functional acts to non-functional acts and vice versa, with a further disconnection from environmental contingences (Boyer and Lienard, 2006). This specific formal structure of compulsive rituals is shared by ritual behavior in non-human animals and in human cultural rituals (Tonna et al., 2019), strongly suggesting a strong continuity in proximal mechanisms. Both ethological and psychopathological data indicate that such highly conserved formal features share homologous neural underpinnings, lying in the basal ganglia loops (Graybiel, 2008).

Interestingly, our study failed to find any association between the structure of compulsive rituals and psychopathological variables of OCD. Particularly, the formal features of OCD rituals did not result correlated with OCD severity or with the level of the patient's insight on the compulsions. We speculate that the structural invariance of ritual reflects its long evolutionary history (encompassing vertebrate phylogeny and perhaps, up to invertebrates). In other words, compulsions represent innate, pre-programmed behaviors inappropriately or excessively "released" in psychopathological conditions (Rapoport et al., 1994), whose formal features are "hardwired" in human brain, thus not shaped by underlying psychopathology personality features. With regard to personality traits, our data seem to suggest a pathoplastic effect of specific personality trait (Borderline, Histrionic and Obsessive) on formal aspects of compulsions.

An association was found between severity of depression in OCD patients and duration (total duration and duration of FA) of ritual compulsions. We argue that specific psychomotor symptoms of depression (namely psychomotor retardation) (Sobin and Sackeim, 1997) may increase the duration of ritual, with an overall slowing down of the action flow and with a tendency to repetition of FA.

Finally, an important relationship was found between psychotic vulnerability, namely the severity of basic symptoms (FBF total score) and formal structure of compulsions. Basic symptoms are subtle, subjectively experienced disturbances in mental processes including thinking, speech, attention, perception, drive, stress tolerance, and affect. Particularly, The FBF focuses on fluctuating cognitive micro-symptoms such as mild derealization, cognitive gliding and loss of automatisms (Süllwold, 1986). They are regarded as an immediate symptomatic expression of the neurobiological processes underlying psychosis and the earliest form of self-experienced symptoms. In contrast, attenuated and overt psychotic symptoms are assumed to develop later, as a result of poor coping with initial symptoms, such as basic symptoms, or stressors, when a vulnerable individual's protective mechanisms are overstrained (Schultze-Lutter and Theodoridou, 2017). In our study, higher severity of basic symptoms was associated with an overall complexity of ritual behavior (total number of single action units, number, duration and repetition of both functional and non-functional acts). That is, the more schizophrenic vulnerability arises at the subjective level of pre-psychotic self-experiences, the more compulsive behavior becomes complex, redundant, slowed down (and thus cognitive demanding), ultimately emphasizing its structural characteristics.

The association between schizophrenia spectrum and OCS is extensively reported in literature. Co-morbid OCD is diagnosed in 8-32% of patients with schizophrenia. Rates of co-occurrence appear to increase in "soft" schizophrenia spectrum, with up to 35% of patients with schizotypal personality disorder having a co-diagnosis of OCD (de Haan et al., 2013). Moreover, early-onset OCD often precedes the clinical onset of psychosis, significantly increasing risk for schizophrenia (Cederlöf et al., 2015).

Interestingly, the severity of basic symptoms is not related to the severity of obsessive symptoms; on the other hand, the severity of OCS is not associated to a more complex structure of ritual compulsions. Therefore, the relationship between basic symptoms and structural complexity of rituals is not due to the severity of OCS. Altogether, in OCD patients with a psychotic vulnerability, ritual compulsions tend to be structurally more articulated and demanding independently from an increase of OCS severity. The complex relationship between schizophrenia vulnerability and ritual compulsions may be viewed at the light of either a pathoplastic or a vulnerability model (Tonna et al., 2015). That is, compulsive rituals may cover an underlying schizophrenia vulnerability, perhaps preceding the first psychotic symptoms and later shaping the clinical presentation of the disease. The emphasis of ritual features in OCD patients at-risk for psychosis is in line with the hypothesis of a "homeostatic" function of ritual behavior. We speculate that in OCD patients, an increase of subjective experiences of perception, thinking, speech and memory, of cognitive control of action and of proprioception, along with the development of transition sequences to psychosis (Klosterkötter, 1992), may be associated to a more ritualized compulsive behavior, as a counterbalancing mechanisms of underlying psychotic vulnerability. Consistently, it has been found that in low-level disorganization schizophrenia mild OCS may act as an "ordering" and stabilizing factor with a positive impact global functioning (Tonna et al., 2016b, 2016). In OCD patients with psychotic proneness, the same counterbalancing mechanism may be at work with an intensifying of ritual structure in compulsive behavior at increasing levels of pre-psychotic subjective experiences, but not necessarily associated with a worsening of OCD severity.

Finally, more severe childhood trauma experiences resulted associated with a more complex structure of compulsions, namely, a higher number of total acts (both FA and NFA), and a higher repetition of NFA with more switches from FA to NFA. Once again, this process of "complexification" of ritual behavior is independent from the severity of OCS. A link between childhood trauma and "obsessive neurosis" was first postulated by Freud (1913). This finding is in line with recent research (de Silva and Marks, 1999; Mathews et al., 2008; Briggs and Price, 2009; Miller and Brock, 2017), suggesting a strong association between different types of childhood trauma (emotional abuse and neglect) and the onset of OCS. As we have seen (chapter 1) 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 negative emotions and anxiety (Miller and Brock, 2017). At the same time, compulsive rituals permit to regain a "feeling" of control and predictability over the psychosocial "high-entropy" state due to past trauma experience. Both motor and cognitive mechanisms might be involved. In fact, across taxa, the repetition of non-functional acts enhances behavioural plasticity in order to deal with environmental unpredictability (Eilam, 2015). Moreover, repetitive and rigid physical action have an anxiolytic effect for itself (Lang et al., 2015; Anderson and Shivakumar, 2013). During a motor task, 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). That is, the cognitive effort on the correctness of the “ordered” movements represents a signal to the self of one’s control over a situation. On the other hand, the focalization of cognition to the rigid rules of ritual may divert attention from negative emotions such as anxiety, uncertainty and stress (Hobson et al., 2018). In this connection, it has been hypothesized that the rigid repetition during ritual performance lead to a swamping of working memory that temporarily reduces anxiety (Boyer and Lyenard 2006). Even though motor and cognitive components appear to be intertwined, from an evolutionary perspective rituals primarily appears as a motor phenomenon, as demonstrated by the finding that repetitive physical action (rather than cognitive demands) is mostly responsible for reducing physiological arousal due to anxiety-related unpredictability (Karl and Fischer, 2018). The sensorimotor experience of engaging in sequenced actions that are rigid, formal and repetitive, coupled with the motor control required to enact these actions, per se satisfies a fundamental need for order and control.

Altogether, in OCD patients, underlying disorganizing processes at different levels, both biological (schizophrenia vulnerability) or psycho-social (childhood trauma), are associated to a more complex motor pattern of ritual behavior. This relationship is uncoupled from OCD severity. We argue that, such mechanism reflects the ultimate causes (i.e. the adaptive significance) of ritual behavior, i.e. its homeostatic function in conditions of unpredictability. Such counterbalancing mechanism, probably lying upon a biological vulnerability to ritual compulsions, may exert an important role in shaping the clinical presentation and course of different psychopathological trajectories, both interacting and “covering” other symptom dimensions.

Table 1. Socio-demographic and clinical features of the sample of patients

	OCD Patients (N=21)	
	n	**%**
Gender		
Male	12	57.1
Marital status		
Not married	13	61.9
Married	8	38.1
Working status		
Unemployement	6	28.6
Employement/Student	15	71.4
Living status		
Alone	7	33.3
With parents/with partner	14	66.7
		Mean ± SD
Age		47.95 ± 14.53
Education years		12.90 ± 2.77
Psychopathological variables		
SOFAS (total score)		63.67 ± 14.05
YBOCS (total score)		20.90 ± 7.47
HAM-D (total score)		5.52 ± 3.70
BABS (total score)		7.48 ± 4.19
FBF (total score)		24.60 ± 23.66
Personality features		
Cluster A		
Paranoid traits		1.06 ± 1.29
Schizoid traits		.53 ± 1.80
Schizotypal traits		1.24 ± 1.48
Cluster B		
Narcissistic traits		1.00 ± 1.70
Histrionic traits		.12 ± .33
Borderline traits		.18 ± .53
Antisocial traits		.00 ± .00
Cluster C		
Avoidant traits		1.82 ± 1.47
Dependent traits		1.06 ± 1.35
Obsessive-Compulsive traits		3.38 ± 1.56
Depressive traits		.71 ± 1.10

Table 2. Comparison between OCD rituals and control behaviors in the form of ritual

	OCD Patients (N=21)	**Control (N=21)**		
	Mean ± SD	*Mean ± SD*	*T*	*p*
Acts *(n)*	9.67±5.09	6.71±4.83	1.98	.061
FA *(n)*	5.86±3.29	5.57±3.60	.27	.790
NFA *(n)*	3.62±3.26	.76±1.37	3.70	**.001**
Modifiers *(n)*	15.90±25.59	7.67±11.28	1.35	.185
Total Duration	52.50±64.38	12.57±15.96	2.76	**.009**
FA Duration	32.79±45.42	11.52±15.36	2.03	**.049**
NFA Duration	19.44±21.62	1.10±2.53	3.86	**.000**
Repetitions FA	25.10±28.28	10.33±13.14	2.17	**.036**
Repetitions NFA	13.48±14.12	1.48±3.37	3.79	**.001**
From FA to NFA	2.05±1.32	.24±.44	5.96	**.000**
From NFA to FA	1.43±1.333	.05±.22	4.71	**.000**
Length FA	3.39±3.53	5.57±3.53	-2.00	.052
Length NFA	2.28±2.26	.36±.76	3.70	**.001**

	1.	2.	3.	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1 BABS	-																											
2 YBOCS	**.835****	-																										
3 STYPL	**.763****	**.631****	-																									
4 OBCMP	**.802****	**.602****	.391	-																								
5 PARND	-.252	-.306	-.423	-.207	-																							
6 SZOID	-.219	-.391	-.216	-.190	**.591***	-																						
7 NARCI	**-.704****	**-.560***	-.415	**-.594***	-.284	-.031	-																					
8 HISTR	-.459	-.245	-.249	**-.536***	-.307	-.169	0.444	-																				
9 BORDL	-.137	.180	-.235	.040	-.107	-.159	-.070	**.586***	-																			
10 AVOID	**.669****	**.655****	**.564***	.378	.137	.021	-.703**	-.211	.043	-																		
11 DEPEN	.453	**.557***	.202	.175	-.038	-.376	-.384	-.156	-.103	**.639****	-																	
12 DEPRS	.339	.292	.435	.142	.056	-.161	-.367	-.240	-.227	.467	.349	-																
13 SOFAS	-.190	-.092	-313	-.153	.088	-.189	-.137	.377	.336	-.382	-.256	-.244	-															
14 HAM-D	-.065	.051	-.344	-.036	-.097	-.381	.030	.429	.226	.176	**.532***	-.050	.157	-														
15 FBF	-.034	.030	-.166	.265	-.142	0.26	-.090	.357	**.750****	.229	-.146	-.456	-.072	.313	-													
16 Acts	.219	.279	-.108	**.550****	-.142	-.343	-.251	.060	**.565***	.163	.068	.040	.059	.416	**.597****	-												
17 FA	.143	0,235	-.270	.409	-.179	-.244	-.101	.088	.334	.035	.138	-.203	.204	**.566****	**.469***	**.788****	-											
18 NFA	.248	.230	.175	**.510***	-.173	-.228	-.217	.036	**.539***	.132	-.167	.148	-.114	-.028	**.518***	**.693****	.153	-										
19 Modifiers	.158	.301	.067	.203	-.350	-.184	-.207	.434	**.725****	.343	.217	-.032	-.026	.421	**.628****	**.594****	.417	**.510***	-									
20 Tot D	-.047	.165	-.141	.061	-.354	-.207	-.087	**.633****	**.865****	.125	.082	-.131	.221	**.499***	**.648****	**.549****	**.452***	.413	**.894****	-								
21 FA D	-.086	.137	-.194	-.004	-.311	-.185	-.078	**.632****	**.834****	.124	.126	-.238	.249	**.536***	**.644****	**.490***	**.477***	.272	**.867****	**.981****	-							
22 NFA D	.038	.200	-.003	.182	-.396	-.219	-.088	**.555***	**.820****	.110	-.049	.106	.130	.347	**.582****	**.602****	.341	**.657****	**.842****	**.916****	**.821****	-						
23 R FA	.027	.254	-.164	.112	-.235	-.113	-.105	**.495***	**.741****	.153	.100	-.295	.225	**.540***	**.616****	**.587****	**.643****	.277	**.863****	**.881****	**.905****	**.727****	-					
24 R NFA	.120	.283	.009	.297	-.289	-.131	-.159	.467	**.857****	.142	-.112	.011	.139	.267	**.640****	**.663****	.391	**.709****	**.844****	**.872****	**.783****	**.952****	**.764****	-				
25 L FA	-0,177	.010	-.292	-.113	.088	-.208	.055	-.075	-.095	-.083	.173	.063	.188	.450*	-.058	.288	**.587****	-.362	-.011	.084	.166	-.094	.268	-0,123	-			
26 L NFA	.022	.117	.228	-.039	-.113	-.175	.048	-.055	.129	-.165	-.271	.033	.023	-.368	-.093	-.160	**-.462***	.284	-.083	-.115	-.172	.021	-.255	.073	-.353	-		
27 From FA to NFA	.393	.375	.096	**.547***	-.109	.000	-.251	.000	.447	.161	-.035	-.128	-.010	-.046	.333	.418	.128	**.630****	**.433***	.267	.187	.397	.285	**.545***	**-.485***	.317	-	
28 From NFA to FA	.402	.282	.251	.400	-.051	.159	-.319	.044	.273	.303	-.086	.034	-.043	-.099	.172	.230	-.020	.444*	.337	.185	.120	.306	.162	.400	**-.499***	.289	**.844****	-

Note. **p≤.01; *p≤.05; YBOCS=Yale Brown Obsessive Compulsive Scale; HAM-D=Hamilton Depression Rating Scale; FBF= Frankfurter Beschwerde Fragebogen; BABS=Brown Assessment of Beliefs Scale; SOFAS=Social and Occupational Assessment Scale; PARND=Paranoid; SZOID=Schizoid; STYPL=Schizotypal; NARCI=Narcissistic; HISTR=Histrionic; BORDL=Borderline; OBCMP=Obsessive Compulsive; AVOID=Avoidant; DEPEN=Dependent; DEPRS=Depressive; FA=Functional Acts; NFA=Non Functional Acts; Modif=Modifiers; Tot D=Total Duration; FA D= Functional Acts Duration; NFA D=Non Functional Acts Duration; R FA=Repetitions of Functional acts; R NFA=Repetitions of Non Functional Acts; L FA=Mean Length of Functional Acts; L NFA=Mean Length of Non Functional Acts

Table 3: Pearson’s correlation among psychopathological variables and formal aspects of ritual

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.
1. CTQ	-														
2. EA	.654**	-													
3. FA	.715**	.272	-												
4. SA	.558**	.014	.760**	-											
5. EN	.871**	.616**	.618**	.481**	-										
6. Acts	.583**	.101	.612**	.663**	.605**	-									
7. FA	.468*	.162	.474*	.454*	.452*	.788**	-								
8. NFA	.516*	.031	.530*	.591**	.544*	.693**	.153	-							
9. Tot D	.369	.091	.038	.067	.125	.549**	.452*	.413	-						
10. FA D	.331	.086	-.007	.010	.046	.490*	.477*	.272	.981**	-					
11. NFA D	.405	.090	.132	.176	.270	.602**	.341	.657**	.916**	.821**	-				
12. R FA	.341	.074	.134	.108	.082	.587**	.643**	.277	.881**	.905**	.727**	-			
13. R NFA	.509*	.038	.308	.336	.302	.663**	.391	.709**	.872**	.783**	.952**	.764**	-		
14. From FA to NFA	.477*	-.146	.494*	.532*	.412	.418	.128	.630**	.267	.187	.397	.285	.545*	-	
15. From NFA to FA	.172	-.361	.250	.262	.187	.230	-.020	.444*	.185	.120	.306	.162	.400	.844**	-

Note. **p≤.01; *p≤.05; FA=Functional Acts; NFA=Non Functional Acts; Tot D=Total Duration; FA D= Functional Acts Duration; NFA D=Non Functional Acts Duration; R FA=Repetitions of Functional acts; R NFA=Repetitions of Non Functional Acts

Table 4: correlations between formal features of compulsions and childhood trauma

Formal structure of cultural rituals

1. Introduction

Classical anthropologic classifications posit different forms of cultural ritual: initiation rites or rites of passage (e.g. birth, initiation, funerals), propitiatory (e.g. sacrifice rites to receive protection of a deity), apotropaic (e.g. preventive practices to ward off evil or misfortune), therapeutic (ritual practices for illnesses), recurring or periodic rites (e.g. seasonal rites) (Lehmann and Myers, 1993). Despite their multi-faceted and symbolically-rich manifestations, human collective rituals share underlying common formal features (Dulaney and Fiske, 1994): internal repetition and redundancy, "scriptedness", detachment from a pragmatic goal (Lienard and Lawson, 2008). Moreover, cultural rituals involve precise spatiotemporal arrays. Ritualized motor performance primarily serve for orientate spatiotemporal parameters, rigidly demarcating sacred and profane times and spaces (Eliade, 1959). 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 Lienard, 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 and OCD compulsions, 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 Lienard, 2006). During ritual performance, ordinary actions are adopted in different contexts and transformed into symbolic expression to be 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. The fidelity to the internal rules of ritualized practice (“scriptedness”) is fundamental in the perception to really achieve a change of state or to do something effective (Hermann et al., 2013). Rather, the efficacy of ritual is strengthen if the performance itself contains elements that make it clearly identifiable as ritual (Legare and Souza, 2012), even though rituals lack overt instrumental purpose and their actions are not immediately causally linked to the stated goal. Therefore, on the one hand ritual motor acts are imbued with symbolic meanings, but on the other, they remain refractory to logical explanations retaining a “causal opaqueness” (Kapitány and Nielsen, 2015). Therefore, as in OCD compulsions, the central element of ritual practice is the precise way by which the motor action flow is organized, regardless to a possible explanation due to a magical thought tendency in OCD or a mythological construction in collective rituals.

With regard to the contents of cultural rituals, the ordinary or physiological acts invariably recurring in ritual behavior typically concern the action cleansing or washing, checking the environment or delimiting space, which are strikingly similar to symptom dimensions of OCD compulsions (Dulaney and Fiske, 1994).

Despite different authors have emphasized the similarity in form and contents between OCD compulsions and cultural rituals (Freud, 1961; Dulaney and Fiske, 1994; Boyer and Lienard, 2006), a comparative study between these two types of ritual with regard to the formal structure of the action flow has been scarcely addressed.

Therefore, the aim of the present study was to compare the motor action flow of ritual behavior in human cultures and OCD patients in order to highlight differences and similarities in the underlying formal structure.

2. Methods

2.1 Procedure

Cultural rituals: We collected the videotapes of human collective rituals from different cultures in order to compare the structure of cultural ritual behaviour with corresponding ritual compulsions of

OCD patients. The analysis of cultural behavior was supported interviewing people from the same cultural background of the examined rituals, in order to acquire an exhaustive comprehension of the cultural significance of the ritual acts.

OCD patients: all participants were recruited from the Psychiatric Unit of the University Hospital of Parma from July 2017 to July 2019. Patients were included in the study if 1) they were aged older than 17 years; 2) they received a diagnosis of Obsessive-Compulsive Disorder (OCD), according to DSM-IV criteria (American Psychiatric Association, 2000); 3) a written informed consent to study participation was obtained. Patients were excluded if they were affected by 1) a current mental disorder related to a general medical condition or to a drug or alcohol abuse or dependence; and 2) a cognitive disorder (Mini-Mental State Examination score lower than 25), which could impair the compliance with testing procedures.

Behavior was scored using “the Observer” (Noldus Information Technology, Wageningen, the Netherlands), a software for ethological descriptions.

Functional and non-functional acts: We listed the acts that comprised each ritual. Acts performed were classified as “functional” if they were considered as being essential to the performance of the task. Acts were classified as “non-functional” if they were considered as being not compulsory for the task. For each OCD and cultural ritual performance, the following parameters were extracted from the video files: ritual duration; incidence and duration of all acts; acts repertoire (number of different acts, excluding repetitions); incidence and mean duration of shared and unique acts; chain length of consecutive shared acts and chain length of consecutive unique acts; incidence of switching between shared and unique acts; frequency distribution of act durations.

Each ritual was classified in light of the main physiological act at the basis of ritual behaviour (for example, ritual purification was labelled as “washing ritual”) in order to compare cultural rituals with corresponding compulsive rituals of OCD patients, matched for age and gender.

2.2 Statistical analysis

T-test was adopted to compare cultural rituals and corresponding OC rituals.

3. Results

Ten cultural rituals were collected. Their cultural background and their classification based on the main physiological act represented are reported in Table1. Their formal structure was compared with equal number of corresponding OCD compulsions (washing, ordering and control compulsions).

3.1 Comparison between cultural and corresponding OCD compulsions

No differences were found in formal features between cultural and compulsive rituals with the exception of washing compulsions, which differed from corresponding cultural rituals for a longer total duration of ritual behaviour due to a longer duration and repetition of functional acts (FA) (Tables 2-3-4).

4. Discussion

The present study was aimed at investigating the formal structure of human collective rituals with respect to OCD compulsions; particularly, to assess whether the motor pattern of cultural rituals might differ from that of compulsive rituals in OCD patients.

Our results suggest that cultural and compulsive rituals share identical structural features, which differ from corresponding physiological acts with respect to: 1) chunking of action flow with rigid repetition of single action-sequences; 2) inflation of NFA and 3) loss of automaticity and diversion of attention to the act itself (the “script” of the performance).

This finding would confirm a continuity in proximal mechanisms between OCD compulsions and cultural rituals. Moreover, exactly like compulsive rituals (Zohar and Felz, 2001), also human collective rituals appear to present a structural invariance across cultures (Dulaney and Fiske, 1994), thus supporting the hypothesis that cultural rituals lie on biological pre-programmed behavioural patterns, i.e. an innate tendency to ritual behaviour driven by the biological constrains of our species.

Interestingly, the unique differences were found comparing cultural “washing” rituals (i.e. concerning religious practices of ablution and purification) with OCD washing compulsions. Psychopathological compulsions differed from the corresponding cultural rituals for a longer total duration of ritual behaviour, due to a longer duration and repetition of functional acts (FA). We interpret the duration of a single act as an index of “thoughtfulness” (Eilam et al., 2006), i.e. an indicator of the cognitive efforts directed to the physiological act at the basis of ritual behaviour, that is inversely related to the level of automaticity of the performance. Washing rituals in OCD patients appear more cognitive demanding with respect to the corresponding cultural rituals. We speculate that the familiarity to the cultural contents of the ritual performance, which on the one hand increases the perceived efficacy of ritual itself (Anastasi and Newberg, 2008), on the other, would favour a return to a major automation of the action-units, especially for functional acts concerning cleaning or washing practices. This does not mean that cultural rituals become automatic action sequences, rather that the familiarity with the internal rules (the “script”) of the ritual as well as a sort of perceived intimacy with the cultural and symbolic framework of ritual probably make ritual performance more automatic (especially for the execution of functional acts).

CATEGORY	CULTURAL RITUAL	RELIGION
Contamination/Cleaning (Washing)	Foot washing	Catholic
	Epiphany (Renewal of Baptesimal Promises)	Orthodox
	Netilat Yadayim	Judaism
	Wudu	Islam
	Tayammum	Islam
	Temizu	Shinto
Symmetry/Ordering	Eucharist	Catholic
	Novice friar clothing	Catholic
Checking/ Control	Wearing Talled and Tefillin	Judaism
	Entering Church	Orthodox

Table 1: Cultural rituals and corresponding ordinary acts

	Washing Compulsion (N=6)	**Cultural ritual (N=6)**		
	Mean ± *SD*	*Mean* ± *SD*	*T*	*p*
Acts *(n)*	12.33 ± 6.59	9.83 ±4.26	.780	.453
FA *(n)*	8.50 ± .3.39	6.33 ± 4.23	.979	.351
NFA *(n)*	3.00 ± 4.52	3.50 ± 2.66	-.234	.820
Modifiers *(n)*	12.17 ± 7.98	2.67 ± 2.07	2.82	**.018**
Total Duration	57.33 ± 21.02	25.61 ± 16.44	2.91	**.016**
FA Duration	40.17 ± 14.72	17.55 ± 17.33	2.44	**.035**
NFA Duration	17.17 ± 12.80	8.07 ± 5.98	1.58	.146
Repetitions FA	33.33 ± 16.08	14.50 ± 12.79	2.24	.**049**
Repetitions NFA	13.17 ± 12.32	5.83 ± 3.49	1.40	.191
From FA to NFA	1.83 ± 1.83	2.50 ± 1.22	-.74	.476
From NFA to FA	1.33 ± 1.37	2.83 ± 1.70	-2.04	.068
Length FA	6.11 ± 5.77	4.08 ± 2.21	.805	.440
Length NFA	1.08 ± .80	1.97 ± .91	-1.79	**.103**

Table 2: comparison between washing compulsions and corresponding cultural rituals

	Order Compulsion (N=2)	**Cultural ritual (N=2)**		
	Mean ± *SD*	*Mean* ± *SD*	*T*	*p*
Acts *(n)*	13.50 ± 0.7	9.00± 4.24	1.480	.277
FA *(n)*	7.00 ± 2.83	6.00 ± 4.24	.277	.808
NFA *(n)*	6.50 ± 3.54	3.00 ± 0.00	1.400	.296
Modifiers *(n)*	25.00 ± 8.48	1.00 ± 1.41	3.946	.059
Total Duration	73.50 ± 3.53	65.45 ± 0.21	3.214	.085
FA Duration	33.00 ± 8.48	36.40 ± 28.50	-.162	.886
NFA Duration	38.50 ± 14.85	29.04 ± 28.29	.418	.716
Repetitions FA	19.50 ± 2.12	6.50 ± 4.95	3.414	.076
Repetitions NFA	20.00 ± 7.07	3.00 ± 0.00	3.400	.077
From FA to NFA	3.00 ± 0.00	1.50 ± 0.71	3.000	.095
From NFA to FA	2.50 ± 2.12	1.00 ± 0.00	1.000	.423
Length FA	2.12 ± 1.24	5.75 ± 6.01	-.835	.491
Length NFA	1.79 ± 0.64	1.50 ± 0.00	.648	.583

Table 3: comparison between order compulsions and corresponding cultural rituals

	Control Compulsion (N=2)	**Cultural ritual (N=2)**		
	Mean ± *SD*	*Mean* ± *SD*	*T*	*p*
Acts *(n)*	5.00 ± 0.00	15.00 ± 15.56	-.909	.459
FA *(n)*	2.50 ± 0.71	6.50 ± 7.78	-.724	.544
NFA *(n)*	2.50 ± 0.71	8.50 ± 7.78	-1.086	.391
Modifiers *(n)*	0.00 ± 0.00	2.50 ± 3.54	-1.000	.423
Total Duration	12.50 ± 7.78	75.93 ± 92.77	-.948	.443
FA Duration	3.21 ± 1.12	40.73 ± 56.51	-.939	.447
NFA Duration	8.53 ± 4.91	34.20 ± 36.26	-.992	.426
Repetitions FA	3.00 ± 0.00	7.50 ± 9.19	-.692	.560
Repetitions NFA	4.50 ± 2.12	17.00 ± 11.31	-1.536	.264
From FA to NFA	1.00 ± 0.00	4.50 ± 6.36	-.778	.518
From NFA to FA	0.00 ± 0.00	5.00 ± 5.66	-1.250	.338
Length FA	2.50 ± 0.71	1.30 ± 0.42	2.058	.176
Length NFA	2.50 ± 0.71	5.94 ± 4.32	-1.113	.382

Table 4: comparison between control compulsions and corresponding cultural rituals

Concluding remarks

Formal structure of rituals

FAPs and 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 FAPs and habits 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.

Ritual behavior maintains the circular and spatio-temporal structure of these pre-programmed (innate or learned) motor displays: first, rituals, 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 Gonner, 2008).

Second, rituals, 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 exaggerated, 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 Lienard, 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. In our studies (both in animals and humans) this may be presumed by the longer duration of the single action-units and of the overall action flow. 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 Lienard, 2006).

Psychopathological compulsions may be conceived as ritualized habitual behavior in that 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 ritual behavior developed from the rearrangement of fixed motor patterns of behavior (FAPs or habits) 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.

Conclusions

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, psychopathological 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 rearranging) 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). As we have seen (chapter 1), developmental genes such as *hox* genes have a highly functionally conserved role throughout phylogeny (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 FAPs and 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.

Ultimately, 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, 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 evolutionally conserved “protective response" (Rapoport et al., 1994; Nesse and Stein, 2012). The function of controlling the environmental (both ecological and social) 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 "disordering" threats (Malinowski, 1922; Sosis and Handwerker, 2011).

The "gap" between biology and culture may be bridged through the assumption that culture, as "extended phenotype" (Dawkins, 1982), continues the ancient paths followed by biological evolution (Levi-Straus, 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 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 ritual behavior 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 inter-disciplinary research to contribute to the discussion.

Concluding, ubiquitously ritual behavior, following its biological constraints, works on maintaining a predictable and ordered (thus safe) environment (ecological and 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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