Rituals, Stereotypy and Compulsive Behavior in Animals and Humans

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ABSTRACT

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Motor rituals in the context of animals in the wild, in captivity, in a model of obsessive compulsive disorder (OCD), in normal humans, and in OCD patients, involve repetitive performance and share analogous form, resulting in confusion between stereotyped, compulsive, and normal behavior. We proposed that durable coupling between rituals and specific locations/objects, and regular transitions between these locations/objects, form a contextual framework for studying rituals. In either animal behavior or OCD patients, rituals are analyzed in five steps: (1) identifying key locations/objects at which rituals are displayed; (2) listing types of movements, acts, or actions displayed at these locations/objects; (3) scoring transitions between locations/objects; (4) scoring order of the set of acts at each location/object; (5) quantifying repetitions across and within locations. By using this approach, it is possible to compare entirely different compulsive rituals, to discriminate locations with compulsive rituals, and to uncover spatiotempral components in OCD patients. The results of this analysis may then serve in characterizing, treating, and assessing the efficacy of treatments in OCD patients.

Keywords: Obsessive-compulsive disorder – quinpirole – amphetamine – pacing stationary – route stereotypy – focused stereotypy – spatiotemporal structure.

Prolog

Obsessive-Compulsive Disorder (OCD) is a severe, chronic psychiatric problem. It was recognized as early as the 16th century, and is now known to have a prevalence rate of 1-3%, which is almost twice that of schizophrenia (Karno et al., 1988; Weissman et al., 1994). ***Obsessions*** refer to recurrent, persistent ideas, thoughts, or impulses that are experienced, at least initially, as intrusive and senseless. ***Compulsions*** are a repetitive, purposeful behavioral ritual, perceived as unnecessary, and performed in response to an obsession, or according to certain rules or in stereotyped fashion. The most common form of OCD behavior is compulsive checking (Henderson and Pollard, 1988; Rasmussen and Eisen, 1992). Compulsive checking rituals may be performed for hours, and in extreme cases may prevent the subject from sleeping or leaving home. Despite their understanding that their obsessive-compulsive behaviors are irrational, patients are unable to control the compulsions, and attempts to prevent the access to the specific location/object of checking (for example, by blocking/removing it) result in a displacement of the compulsion to a new location/object. Surveys on OCD indicate that ethological approach in the study of compulsive rituals may reveal the structure (form) of such behavior, and an understanding of structure may be valuable in uncovering the underlying mechanisms (Reed, 1985). Indeed, studies of human compulsions frequently describe the abundant rate of performance of behavioral patterns using terms borrowed from ethology, such as 'displacement activity' and 'stereotypy' (Insel, 1988), or 'ritualized behavior' (Rapoport, 1990). In one of the early discussions of animal models of OCD, Thomas (Insel, 1988) wrote: "*The available analysis of the phenomenology of compulsive rituals pales before elegant observations of analogous behaviors in fish and birds*", referring to the early studies of Nicolas Tinbergen and Konrad Lorenz, that jointly with Karl Von-Frisch, were awarded the Nobel Prize in 1973. At the other end, the link between animal behavior and abnormal repetitive performance was also apparent to K. Lorenz who wrote: "*My examples of animal behavior will* *remind the psychiatrist and the psychoanalyst of the compulsive repetition of some acts, a symptom of certain type of neurosis*" (Lorenz, 1966; p 160). This link between detailed inspection of animal behavior and pathologic motor behavior was also highlighted in the Karolinska Institute press release that reasoned granting the Nobel Prize to Von-Frisch, Tinbergen and Lorenz, stating that *"The prize winners' discoveries, mainly the results of studies on insects, fishes and birds, have stimulated to comprehensive research also on mammals… Research within these fields has led to important results for, e.g. psychiatry and psychosomatic medicine, especially as regards possible means of adapting environment to the biological equipment of man with the aim of preventing maladaptation and disease" (http://nobelprize.org/medicine/laureates/1973/press.html).* Repetitive performance of motor rituals is the scope of the present survey, aimed at demonstrating that recurring normal behavior, cage stereotypy, drug-induced stereotypies, and behavior of Obsessive-Compulsive Disorder (OCD) human patients feature a similar spatio-temporal structure. Specifically, this survey is aimed at providing a broad view on motor rituals, forming a substrate for assessing the inflated ritual performance in OCD patients and animal models of OCD. We will first describe normal motor rituals, then motor rituals in animal stereotypies and OCD models, and finally, motor rituals in OCD patients.

Repetitive motor rituals: Form and function in normal behavior of animals and humans

Figure 1 (taken from (Hediger, 1964) describes schematic animal territory constructed of various places in which the animal has typical activities: in place A it scent marks, in B it takes a rest, in C it forages, etc. Thus, the territory is conceived of as a set of places, each with a specific set of acts. These places are inter-connected with a network of relatively fixed routs (the "familiar path"; (von-Uexkull, 1957), forming a map-like environment. More-so, behaviors at typical places are performed at a particular, relatively fixed time (Hediger, 1964), and behavior is organized in a predictable itinerary. For example, a fixed itinerary of animals in the wild was revealed in observations of rock hyraxes (*Procavia capensis*; (Serruya and Eilam, 1996). The home site of the observed group of hyraxes was a rocky ramp partially covered with a bush. Before embarking to their morning and afternoon activities, the hyraxes climbed to the external branches of the bush and sit there for a while. Then they descended to the rocky ramp through a few fixed locations ("Doors"). The edge of the bush on the ramp was homogeneous, and there was no apparent reason for the location of these “doors”, yet 80% of the transitions between the ramp and the bush occurred in specific three locations (“doors”). Once on the ramp, the hyraxes tend to stop frequently on few and the same rocks, out of the hundreds rocks of the ramp. On these few rocks they set, lay, or crouched in a few typical postures, and arrived at these location in preferred compass directions from preferred places (rocks) (Serruya and Eilam, 1996). In all, these observations revealed a relatively rigid set of acts that occurred in specific locales that were performed in a regular order (spatiotemporal organization).

A preference to display specific acts in specific spatial locales was observed in many mammalian species. Rhinos (*Diceros bicornis;* (Schenkel and Schenkel-Hulliger, 1969), deer (*Cervus elaphus*; (Hediger, 1964), antelopes (*Redunca arundium*; (Jungius, 1971), and camels (*Camelus dormedarius*; (Schulte and Klingel, 1991) have fixed crouching and resting places that are preserved for considerable periods. Other species repeatedly visit demarcation sites, where they display a typical ritual of marking by urinating, defecating, or secreting scent materials (Henschel and Skinner, 1991; Muller-Schwarze, 1972; Richardson, 1991). Altogether, there is 'territory', 'home range' or 'living range' or 'core activity-area' at which animals execute most of their activity (Fourie and Perrin, 1987; Hoeck et al., 1982; Jungius, 1971; Kauhala et al., 1993). These, together with the example of hyraxes, illustrate that locomotion along relatively fixed paths and displaying specific motor rituals in specific locations are ingrained in the behavior of normal animals in the wild.

The link between specific acts (movements) and specific locations was embedded in many of the colorful descriptions of Konrad lorenz (Lorenz, 1952; Lorenz, 1966), focusing on either the role of motor routines in daily animal life, and on the striking consequences of blocking these rituals. For example, water shrews that were used to jump over a stone that was in their familiar path kept jumping even after removal of the stone by Lorenz, as if the performance of motor template overrides the sensory input that the stone is not there anymore (Lorenz, 1952); p. 127). Another example for the vigor of motor habits in animal behavior is Lorenz's graylag goose, Martina, which grew in his home and was used to sleep at the upstairs bedroom. Martina used to spend the day outside in the yard, and upon entering in the evening the relatively dark house, to walk first to the window and only then climb the stairs to the bedroom. With time, the walk to the window was shortened, finally replaced by a motor habit of just turning the head and neck toward the window before climbing to the bedroom. But then come the thrilling event: "*One evening I forgot to let Martina in at the right time, and when I finally remembered her it was already dusk… as I opened the door she thrust herself hurriedly and anxiously through… ran between my legs into the hall and contrary to her usual custom, in front of me…and starting to climb up… Upon this, something shattering happened: arrived at the fifth step, she suddenly stopped, made a long neck, in geese a sign of fear… then she uttered a warning cry… turn round, ran hurriedly down… like someone in very important mission, on her original path to the window and back… looked around, shook herself and greeted, behavior mechanisms seen in graylags when anxious tension has given place to relief…*" Lorenz summarized this shuttering scene in stating: "*I hardly believed my eyes. To me there is no doubt… the habit had become a custom which the goose could not break without being stricken with fear.*" Lorenz was aware that breaking habits frustrates also humans, as for example, children that tenaciously cling to every detail and become quite desperate if a story-teller diverges in the very least from the text of familiar fairy-tale (Lorenz, 1966), or his own driving habits: "*I once suddenly realized that when driving a car in Vienna I regularly used two different routes when approaching and when leaving a certain place in the city… Rebelling against the creature of habit in myself, I tried using my customary return route for the outward journey and vice versa…The astonishing result of this experiment was an undeniable feeling of anxiety so unpleasant that when I came to return I revered to the habitual route*." Summarizing these examples on the role of fixed motor rituals in animal behavior Lorenz suggested that they resemble compulsive behavior, stating that: "*My examples of animal behavior will remind the psychiatrist and the psychoanalyst of the compulsive repetition of some acts, a symptom of certain type of neurosis…*" (Lorenz, 1966); p. 160).

The astonishing similarities between these rituals in animal and human normal behavior also illustrate a fundamental dichotomy to: i) traveling along regular paths (routes), and: ii) displaying specific rituals in specific locations. For example, the behavior of the hyraxes (see above) was comprised of traveling along regular routes that connect specific locales (places) at which a typical behavior was displayed. The schematic territory (Figure 1) also represents the dichotomy to locales at which specific behaviors (actions) are performed, and a network of regular routes that connect these places.

Figure 1

In a broad level, Figure 1 is an illustration of the organization of behavior in the ***locale space***, where home range, territory or other forms of living area (Hediger, 1964; Hoeck et al., 1982; Immelmann and Beer, 1989) are probably the most familiar structures. In order to study behavior in the locale space, it is enough to refer to the animal as a moving point and ignore the concrete movements of its limbs. For example, the black rhino (*Dicerus bicornis*) travels along three set of routes: i) major routes that mainly lead from grazing areas to water sources; ii) secondary routes that traverse the grazing areas; iii) short routes that extend from the secondary routes to bushes and shrubs. Black rhinos also performed typical set of acts during non-locomotory periods. For example, when crouching in specific resting and sleeping locales, they first botch the ground with their forelegs, they then lay down on one side and after few minutes stand up, and then crouch again but this time of their other side (Schenkel and Schenkel-Hulliger, 1969). The behavior of rhinos illustrate that for studying routes, it is enough to treat the animal as a moving point and describe only its trajectories, whereas for the behavior during non-locomotory periods (stopping at specific locales), a description of the discrete movements of the limbs of the animal are required.

Demarcation is another routine which is typically displayed in particular locales, as described for many species [i.e., the hyena and the panda (Gorman and Trowbridge, 1989); the otter (Rowe-Rowe, 1992); and the black rhino (Schenkel and Schenkel-Hulliger, 1969)]. Antelopes live in large territories which they mark repeatedly. The demarcation ritual in pronghorns (*Antilocapra Americana*; taken from (Walther, 1977) is comprised of three successive steps. First, it sniffs the location while stomping with the forelegs. Second, it keeps the forelegs rooted while stepping forward with only the hindlegs, arching the back and defecating directly on the demarcation location. Third, it holds the hindlegs rooted, stepping forward with only the forelegs, thus stretching the trunk to bring the urethra above the demarcation location and urinating directly on the location (Figure 2).

Figure 2

The above examples illustrate that normal behavior, at least in part, consists of performing particular set of behaviors (also termed acts or actions) at specific, pre-established locations and traveling along regular routes that connect these locations. Such regularities give rise to the question on their mechanistic advantage in normal behavior. A possible mechanistic explanation of fixed routines is minimal involvement of information processing systems, which in turn enables the animal to direct its attention elsewhere and perform the behavioral pattern faster (Fentress, 1976). In other words, behavioral rigidity such as the preference to stop at particular fixed places or to approach specific locations in specific directions allow faster performance or require less attention, enabling to direct more attention to other aspects of the environment (e.g., presence of potential predators). Indeed, we feel more relaxed in driving a familiar road and may direct attention to other activities such as listening to music, but in driving an unfamiliar road, more attention is paid to the road and additional activities are minimized. This linkage between attention and performing rigid motor rituals is bidirectional, and rigid routines or itineraries may be constructed whenever a high concentration is required, as in the case of sport masters or a prayer, that perform rigid intensive rituals during action play or rigorous pray. In all, three conclusions may be derived from the above descriptions of normal and natural behavior: i) motor activity is comprised routes and locales (places); ii) in certain locales, animals normally perform specific acts that are carried out in a fixed 'stereotyped' fashion; and iii) performing 'stereotyped' rituals may be a practical mechanism to concentrate or divert attention.

Rituals in cage and drug stereotypies

Constancy of form in behavior produced through ritualization or uniform repetition of motor patterns is termed *stereotypy* (Immelmann and Beer, 1989), and typically occurs in wild animals in captivity (Hediger, 1964; Meyer-Holzapfel, 1968; Stevenson, 1983), in farm animals (Fraser and Broom, 1990), and after administration of psychoactive drugs (Robbins and Sahakian, 1981). Repetitive performance of a behavior pattern or action in a particular time and place is indeed a conspicuous and indisputable characteristic of stereotypy with rigidity that is rarely matched in normal rituals (as described above) or compulsive performance (as described below). This is illustrated in the behavior of a caged black bear (*Selenarctus tibetanus*) and a caged brown bear (*Ursus arctos*) during continuous 30 minute observation (Tables 1-2). The little variation among repetition attests for rigidity of cage stereotypies that occur just by taking animals that live and forage over a large range and confining them in impoverished, relatively small captive environment. Indeed, caged stereotypy was described in a large spectrum of domestic, farm, and caged species (Dantzer and Normede, 1983; Duncan and Wood-Gush, 1972; Keiper, 1970; Rushen, 1984). It is presumed that caged stereotypies evolve in the restricted captive environment, reflecting boring and dull and constricted environment that induces stress and frustration.

Tables 1 & 2

Caged stereotypy dichotomizes to ***stationary***, which are movements that are executed without progressing in the environment, and ***pacing***, which is based on progressing along fixed paths (Carlstead et al., 1993; Cornin et al., 1986; Cronin and Wiepkema, 1984). Pacing may take the form of repetitive passing of the same path (Carlstead et al., 1993; Wechsler, 1991), which generally is circular or 8-shaped (Hediger, 1964). Stereotyped pacing is very rigid and prevalent in animals that range over large territories in the wild. For example, captive polar bears (*Ursus martimus*) had 2-3 fixed paths in which they traveled with a footfall sequence that was based on accurate stepping on the footprints made during the previous pass of that path (Wechsler, 1991; also illustrated in other bear species in Tables 1 & 2). Stationary movements are more typical in farm animals and pets (Mason, 1991; Rushen, 1984), taking the form of vacuous chewing, side-to-side head movements, eye rolling, yawning, gnawing, licking, etc. (Carlstead et al., 1993; Eichler et al., 1980; Mason, 1991; Rushen, 1984; Terlouw et al., 1992; Wechsler, 1991). Altogether, caged stereotypy, like normal behavior, comprises traveling along relatively fixed paths and displaying specific rituals in specific places.

When animals are treated with psychoactive drugs, they display ***route stereotypy*** which is based on repeated passing of the same few paths (Eilam and Golani, 1994; Muller et al., 1989; Schiorring, 1971), and ***focused stereotypy*** which is based on in-place repeated acts such as licking and biting (Arey et al., 1991; Costall and Naylor, 1975). Thus, the terminology of route and focused stereotypy is equivalent to pacing and stationary in caged animals. (Lyon and Robbins, 1975) proposed that stereotypy develops through increased activity that prevents the animals from completing movements, curtailing single movements or sequences of movements. According to this model, when activity increases, the duration of each movement is shortened until it is not completed and prematurely terminated by the beginning of the next movement. Further increase in activity results in shortening the whole sequence of acts by eliminating movements. These processes were illustrated in the behavior of rats that were trained to avoid electric shock by bar-pressing. When treated with drugs that induce hyperactivity, these rats shortened their behavior to just touching the bar without pressing it enough to prevent the shock. Another illustration is that of stereotyped rats that chewed food without swallowing and digesting it (Lyon and Robbins, 1975). Other studies, however, show an increase in the amplitude of specific movements and an almost identical motor repertoire in both drug- and saline-treated rats (Ben-Pazi et al., 2001), or routes that are longer in stereotyped compared with normal rats (Eilam and Golani, 1994). Together, four parallel processes account for the development of stereotyped motor rituals under drug administration (Ben-Pazi et al., 2001): (a) increase in activity; (b) repetitive locomotion along the same few paths; (c) increase in the incidence of stopping in a few specific places, along with a decrease in stopping at other places; and (d) emergence of relatively fixed motor rituals in stopping places. We therefore argued that stereotypy does not arise from mere changes in the ***content*** of behavior, but also from changes in the ***spatial and temporal organization*** of normal behaviors. Consequently, stereotyped behavior is normal behavior that becomes overly repetitive and is established while losing flexibility (Mason, 1991). In stereotypy, however, movements are structured into short and repetitive sets, compared with the relatively long and diverse sequences in normal behavior (Ben-Pazi et al., 2001). For example, stereotypy in mice was shown to develop from normal activities like jumping or chewing, although these were then detached from the original behavioral context (Wurbel, Stauffacher, & Holst, 1996).

(Mason, 1991) drew three similarities between stereotyped and normal behavior: i) stereotypy is rigid and resistant to changes, as are many normal behaviors such as grooming or display behaviors; ii) stereotypy is purposeless, but so are many normal acts such as habits; and iii) like normal behavior, once stereotypy develops, it becomes detached from the stimuli that evoked it and may appear in entirely different situations. These features constitute the definition of stereotypy as unvarying, repetitive behavior patterns that have no obvious function (Fox, 1965; Immelmann and Beer, 1989; Odberg, 1978). The latter definition conveys two attributes of stereotypy: purposelessness and repetitiveness.

Purposelessness seems an ambiguous facet, hard to assess in animals. The two above examples, of chewing food without swallowing it, and bar touching without preventing electric shock, illustrate a behavior which is performed without obvious purpose. Indeed, the continuous pacing of the same path in caged or drugged animals seems purposeless, but such an attribute is hard to assess, in fact inaccessible in animals. We may train an animal to perform certain behavior in order to reach a certain goal, and utilize this procedural context for discerning the purpose or driving force of the trained behavior. Other activities may be directly linked to obvious function, such as feeding, avoiding predator, mate finding, etc. Thus, it is possible to show that a behavior has function, purpose, or goal. The opposite, however, is not necessarily true and purposeless is generally a subjective presumption. For example, while certain stereotypy, such as pacing a fixed path may be conceived purposeless, this mere performance may result in an indirect benefit such as relief of anxiety (Dantzer and Normede, 1983; Hutt and Hutt, 1965; Mason, 1991; Wechsler, 1991). Similarly, human compulsive patients admit that they gain an anxiety relief by repetitive performance of rituals (Rapoport, 1989a). Accordingly, a beneficial repetitive behavior is not purposeless, and the attribute on lack of direct purpose, at least in animals, is a subjective interpretation which is not a distinctive feature of stereotypy.

While purposelessness is ambiguous, the unvarying and incessant repetitive performance is the conspicuous feature of stereotypy, giving rise to the question of how many repetitions are normal, and how many are required to call a behavior 'stereotyped'. In studying stereotypy in red-backed voles (*Clethrionomys glareolus*), a threshold of 10 repetitions was employed to discriminate stereotypy from normal behavior (Cooper and Nicol, 1991). Accordingly, nine were repetitions presumed "normal", but 10 presumed "stereotyped" behavior. Accordingly, monotonous cooing of doves is a normal, yet stereotyped behavior (Immelmann and Beer, 1989). All in all, the confusion and lack of satisfying definition of stereotypy was nicely summarized by (Robbins, 1977) who found that behavior was described as stereotyped when a repetitive bout of behavior was abided <u>intuitively and subjectively</u>.

The lack of unambiguous distinction between normal and stereotyped <u>animal</u> behavior is also extended to compulsive behavior. Indeed, surveys on compulsive-like behavior in animals, intuitively classify exaggerated performance as compulsive. For example, in describing symptoms of compulsive disorder in dogs and cats, (Luescher, 2004) provides the following description: *"…behaviors categorized as locomotory, oral, aggression, vocalization, amd hallucinatory behaviors. In dogs, locomotory behaviors include circling, tail chasing, jumping in place, chasing light reflections, and freezing; in cats, locomotory behaviors include freezing, sudden agitation and skin rippling, ducking, and circling…*(p.234)" - all may as well be considered as stereotypies for being repetitive and purposeless. While there are doubts whether animal can obsess, or whether an excessive performance in animals is a manifestation of an obsessive compulsive disorder (Frank and Dehasse, 2003), there is a neurobiological support of the notion of animal OCD: anti-compulsive drugs that have been used in medication of OCD human patients reduce apparent OCD symptoms in animals. For example, serotonine re-uptake inhibitors (clomipramine, fluoxetine) have been most effective drug therapy in blocking tail chasing in bull terriers (Moon-Fanelli, 2005), and clomiparamine reduced compulsive symptoms in dogs with canine compulsive disorder (CCD), but treatment for 4 weeks was not curative (Hewson et al., 1998). In all, there seems to be confusion: on one hand a similar efficacy of pharmacotherapy is indicative of similar neuropathology in compulsive behavior in animals and humans; on the other hand, repetitiveness and purposelessness were attributed to both compulsive and stereotyped behavior. Here we propose two traits, flexibility and thoughtfulness (= purposefulness) characterize compulsive-like behavior and distinguish it from stereotypy. In order to illustrate these differences we first describe our rat model of OCD.

We found that after 10 repeated injections (spaced at 3-4 day intervals) of 0.5 mg/kg of quinpirole in a large arena, rats were sensitized to the drug, reaching a level of activity that could be as much as 16-fold higher than that of controls. Yet, this elevated level of activity was confined to a restricted portion of the arena, seemingly reflecting shrinkage of the attended space. In the restricted portion of the arena, rats locomoted hurriedly from place to place, seemingly exploring the environment with unbounded curiosity. Indeed, a conspicuous characteristic of quinpirole-treated rats was that they never habituated, rather kept in repeatedly visiting the same few places without habituation or fatigue (Eilam and Szechtman, 2005). We showed that the behavior of quinpirole rats is characterized by: i) there were one or two places/objects to which the rats returned excessively more often than to other places/objects in the environment; ii) the time to return to these preferred places/objects was excessively shorter than to other places/objects; iii) excessively few places were visited in between returns to the preferred places/objects; iv) a characteristic set of acts was performed at the preferred place/object, which were differ from the acts performed at other locations/objects; v) activity was altered when the environmental properties of the places/objects were changed. We then proposed that these characteristics of quinpirole-treated rats are also applicable for compulsive rituals in human patients (Szechtman et al., 1998). A thorough discussion of the potential of quinpirole rats as a model of OCD is available elsewhere (Szechtman et al., 1999; Szechtman and Eilam, 2004; Szechtman and Woody, 2004).

To the present work, we propose that repetitive behavior in quinpirole rats is relatively flexible and purposeful, while stereotypy is relatively rigid and is considered purposeless. These differences are implicit in the trajectories of locomotion, sequence of stops and movements shown for a quinpirole and an amphetamine rat (Table 3). As shown, the trajectories and sequence of stopping places in the amphetamine rat are entirely rigid and predictable, whereas in quinpirole rat they are flexible, with only two of the 10 repetitions being similar. Same applies for the sequence of movements shown for each of these rats in the two most visited places. The amphetamine rat did not display vertical movements, continuously maintaining snout contact with the arena surface. Since grooming ceases under amphetamine and forward progression is mutually exclusive to stopping, the amphetamine rat displayed only side to side lateral movements which are the sole content of its behavior in all stopping places at this phase of drug action (30 min after subcutaneous injection of 5 mg/kg). In contrast, quinpirole rats had a variety of vertical movements (e.g. – head movements, rearing on hind legs, head dipping, climbing on objects with only forelegs or with all legs) and these were blended with lateral movements to sequence that differ between the two locations. Yet, each place had certain characteristics in movement the sequences; for example, in place #30 all sequences started with upward vertical movement (V_u) and ended with a clockwise lateral movement to direction 6 (C_6). Moreover, the compulsive-like performance in quinpirole rats is limited to the preferred locations (stopping places), whereas in other, non-preferred locations, their behavior did not differ from that of saline-treated rats (Ben-Pazi et al., 2001). In other words, compulsive-like behavior in quinpirole rats is coupled with only few specific locations. Altogether, both the sequence of stopping places and of the movements at these stopping places are flexible under quinpirole but rigid under amphetamine, thus meeting the first of the above attributes on the difference between compulsive ad stereotyped display in animals.

Table 3

The second attribute, that compulsion is purposeful whereas stereotypy is considered purposeless, is also based on the flexibility of behavior in quinpirole rats. A great care should be taken in drawing parallels between behavior of Obsessive-Compulsive Disorder (OCD) human patients and motor routines in animals, as the diagnosis of OCD depends on cognitive symptoms inaccessible in freely moving animals (Mason and Turner, 1993). Obviously, obsession, which are repetitive ideas or thoughts are not accessible in animal behavior. Compulsions are a repetitive, purposeful behavioral ritual, perceived as unnecessary, and performed in response to an obsession. Indeed, we can describe repetitive display in animals, but can we also infer that these repetitions are performed in response to a repetitive idea or thought? We suggest that the flexibility in behavior of quinpirole rats attest that this is not motor automatism. In other words, the rats are not repeating a fixed sequence of movements (as do amphetamine animals) but rather follow a "general plan" in which they have a certain level of flexibility (see, for example, the quinpirole rat shown in Table 3 that has a certain flexible traveling schema and certain flexible set of movements in each place). Since a 'plan' is compatible with 'idea' or 'though', the repeated display in quinpirole rats may be presumed as an animal model of compulsive behavior (for further discussion on the appropriateness of quinpirole rats as a model of OCD, see (Eilam and Szechtman, 2005). Further support for the notion of "general plan" arises from the coupling of comp ulsive-like behavior in quinpirole rats with only specific locations. Indeed, quinpirole rats seem compulsive when visiting the preferred locations, but once visiting other, non preferred locations, their behavior does not differ from that of saline treated rats (Ben-Pazi et al., 2001). Quinpirole rats thus look normal in part of the environment but seem compulsive in other parts, as if the action of the drug was differential and place-specific. The similarities and differences between stereotyped and compulsive animal behavior, as reflected in the behavior of amphetamine and quinpirole rats, are summarized in Table 4, illustrating that there is a difference between stereotypy and compulsion, but this difference is apparent only when the limelight is on the spatiotemporal structure of behavior.

Table 4

Ethological study of rituals in OCD patients

So far we have described motor rituals in natural, captive, and drug treated animals, surmising that these descriptions are beneficial for understanding the structure and malfunction in human OCD. Here we illustrate how tools that were developed in animal studies may be utilized in studying human compulsive behavior. For this we follow four steps: i) discerning the building blocks of a malfunctional compulsive ritual and comparing it with a normal functional performance; ii) comparing the structure of rituals in OCD patients to subsequent performance of the same rituals by the same patient; and iii) quantifying different rituals of different patients, compared with normal performance.

(i) The building blocks of malfunctional compulsive rituals

The common thread in all above descriptions, from those of Konrad Lorenz to those of quinpirole and amphetamine rats, is the distinction of specific areas or objects, and analysis of the set of acts (movements) performed at these specific objects/areas. We assumed that the key for analyzing and understanding OCD rituals could relay on identifying places and acts in these rituals. Consequently, we applied the same analyses of rats on rituals of OCD patients. This procedure is illustrated in a compulsive ritual of car locking. First, the patient's ritual was divided to the acts performed inside the car (Table 5a) and those performed outside the car (Table 5b), since the ritual took place in these two distinct domains (inside and outside the car). Then, the locations at which the patient displayed acts were identified (top rows in Tables 5a and 5b). Specifically, the acts inside the car were further classified according to the object/area at which they were executed: ignition key, light switch, steering wheel, and gear stick. Finally the set of acts in each location was scored, represented by a simple verbal description of the acts at each object/area. The result entire description, as shown in Table 5a,b provides the sequence of acts, highlighting the repetitive performance of this patient. This is conspicuous when compared with a control person who was asked to execute the same action: switch off the engine and then lock the gear stick (Table 5a, bottom). The same methodology was then applied in analyzing the set of acts outside the car (Table 5b), similarly illustrating the performance of a repetitive set of acts in OCD patient, whereas the control person did a simple sequence of these acts with no repetition. The entire sequence of the control person took 17 seconds, whereas that of the OCD patients was more that 12-fold longer (215 seconds). In all, therefore, scrutinizing behavior according the set of acts at each area/object provides a constructive search image for understanding repetitive display in animals and humans suffering of OCD.

Table 5a,b

(ii) The repetitive structure of rituals in OCD patients.

While in Table 5a,b we compared the same action in an OCD patient and in a normal control person, the same method of identifying objects and the set of acts performed at these objects may be also applicable for comparing repetitive rituals of the same patient. Table 6 describes four repetitions of a ritual of nose-blowing in OCD patient. For brevity, characters were assigned to each act in the ritual, and the sequence of these characters (acts) represents the spatiotemporal structure of the ritual. As shown, each repetition of the ritual consists of repeating the same few acts in a relatively fixed order with only few variations. As in quinpirole rats, sequences of acts in this OCD patient comprised a typical structure with a certain amount of flexibility. This structure of behavior is typical in humans suffering from

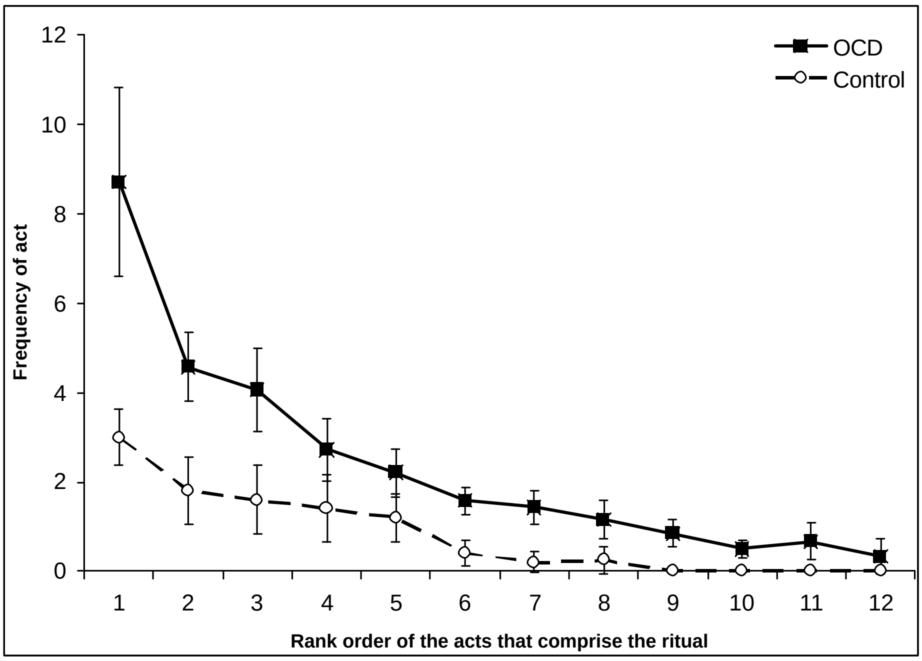
OCD where almost every act, even as simple as hand washing, dish washing, eating, mouth wiping, or door opening, is performed in a constant form and intensity, and is a part of a long set of rituals that severely obstruct normal functioning. Table 6 also illustrates that the rituals are repetitive in two dimensions: (i) across locations; and (ii) within each location/object. Specifically, in Table 6, the first dimension is the regular transitions between objects: first taking a tissue roll, secondly blowing and wiping the mouth, and thirdly handling the used tissue paper. The second dimension is within each location/object (columns), where the patient repeated the same set of acts with minimal variation. These two dimensions are reminiscent of what we saw in animal behavior: repetition across locations is comparable with pacing or route stereotypy (sequence of stops in Table 3a,b or the three postures of the pronghorn in Figure 2), whereas within location/object repetitions are comparable with the sequence of movements performed by the rats in each stopping location (Table 3c,d or the movements leading to each posture of the pronghorn in Figure 2).

Table 6

(iii) Quantifying different rituals of different patients.

A major obstacle in studying compulsive behavior in OCD patients is how to compare different rituals. After all, how can we lump together rituals of hand washing, door locking, dressing, and turning on TV? The above separation of areas/objects and acts provides a relatively simple means for such quantification. We counted the incidence of acts in each place (for example, the number acts in the columns of Table 5a are 6,4,5,13,2 for the OCD patient, and 2,0,0,1,1 for the control). After applying the same count for each ritual, we ranked the incidences from high to low, calculated the mean incidence for each rank of acts in 14 OCD and 5 control rituals (repetitions included). Figure 3 describes the frequency distribution of the ranked number of repetitions of acts in OCD patients and control that were asked to perform the task that was ritualized in the OCD display. These included: hand washing, dishwashing, table cleaning, car locking, door checking and nose cleaning. As shown in Figure 4, OCD rituals comprised up to 3 building block which were repeated significantly more (3-4 fold) than any of the control movements, resulting in the repetitive manner of OCD rituals (= many repetition of same few movements). The conclusions that may be derived from Figure 4 are therefore: i) there are a few (1-3) areas/places/objects at which repetitive acts (building blocks) are performed; ii) OCD rituals may be quantified across distinct rituals; and iii) criteria that were derived from studies in animal behavior are applicable and useful in studying OCD rituals in human patients. The above survey covered the former two conclusions, the latter, on the potential clinical implication is dealt below.

Figure 3



The above analyses concentrated on the act incidence; however, as shown in the quinpirole-rat model, time interval between these acts may be also measured in order to highlight the short time between repetitions of same acts compared with the longer time intervals between other acts. Similarly, the number of acts between repetitions of repetitive acts may be scored and compared with controls, as in the rat model (Ben-Pazi et al., 2001; Szechtman et al., 1998).

Altogether, these measures may provide tools to compare and characterize the severity of OCD, with more obsessive-compulsive patients spending more time in performing each ritual, spending less time between successive repetitions of components of the rituals, and stopping less frequently at other locations/objects.

Epilogue

(Immelmann and Beer, 1989); p. 255) proposed that ritualization, which is the process of development of motor ritual, occurs through "*increase in conspicuousness by simplification and 'exaggeration' of form, repetition (usually rhythmical), emphasis of particular components, slowing down or speeding up of performance, addition of morphological support such as coloration and stereotypy. In contrast to their unritualized antecedents, ritualized behavior patterns typically show considerable constancy in the vigor and rapidity with which they are performed*". This definition, which was formulated on the basis of detailed studies in animal behavior, is perfectly applicable for compulsive behavior in OCD patients. However, the present survey elaborates on this apparent similarity, demonstrating that the spatiotemporal structure of rituals may highlight similarities and differences between human and animal behavior.

The core of similarity is the separation to locations/objects and routes between these locations. This is nicely illustrated in the following excerpts from a dairy of an OCD patient, describing her behavior when switching on the TV: "*Before I start to turn it on, I have to wash and dry my hands. Then I go and touch the corner curtain followed by touching the side of the TV two times. Then I have to go back and wash my hands. When I am finished with that I will look behind the lamp 2 times, go back and wash my hands, come back, move the lamp to the left and look behind it, move the lamp two times to the right and look behind it, go back, wash my hands, and then look in back of the TV on the left 4 times, washing my hands in between each one. Then I look in back of the TV on the right 8 times, wash my hands, and put the TV on* *channel 6. Then I turn the knob from channel 6 to 7, 4 times, and from channel 6 to channel 8, 4 times. Then finally I turn it on. The whole thing probably takes around half an hour*." (Rasmussen and Eisen, 1991)p. 28). This ritual is based on two key locations: the TV and the bathroom, with the patient traveling repeatedly ('pacing') between them, paying 10 visits to the TV and 9 visits to the bathroom. At each location, a typical set of acts is performed – for example, there are 17 repetitions of looking behind the lamp/TV. These and other measures (e.g., time and stopping locations between successive visits to the TV and bathroom) follow the same criteria that were constructed from rituals of a rat model (Szechtman et al., 1999), illustrating that these criteria and descriptive are applicable in studying compulsive behavior in humans.

There are, however, cardinal differences between rituals in humans and in animal behavior. While we may ask people for the purpose of rituals and learn that, for example, they feel relief and ease of anxiety by the mere performance of a ritual, in animals such inquiries are impossible, and we can just presume animal anxiety or its relief, as (Lorenz, 1966) did when interpreting the rituals of his graylag goose Martina. Another mechanism that characterizes human patients is avoidance, where patients try to intentionally avoid the compulsive location in order to evade their need to perform the set of acts at this location/object. For example, a patient with cleaning ritual at his home, slept in the street in order to avoid the house-cleaning rituals ("The secret life of street person"; (Rapoport, 1989b); p. 135). Again, such avoidance of activity is not accessible in animals, and a deviation from the regular ritual or path is always considered as an arbitrary variation.

A great care should be taken in drawing parallels between Obsessive-Compulsive Disorder (OCD) human patients and motor routines in animals, as the diagnosis of OCD depends on cognitive symptoms inaccessible in freely moving animals (Mason and Turner, 1993). However, a search for parallels in underlining mechanisms in OCD and animal motor routines may gain benefits from a consideration of these behaviors strictly at level of motor performance.

Acknowledgments

References

Arey, D., Petchey, A., and Flower, V. 1991. The preparturient behavior of sows in enriched pens and the effect of pre-formed nests. Applied Animal Behaviour Science 31**,** 61-68.

Ben-Pazi, A., Szechtman, H., and Eilam, D. 2001. The morphogenesis of motor rituals in rats treated chronically with the dopamine agonist quinpirole. Behavioral Neuroscience 115**,** 1301-1317.

Carlstead, K., J.L., B., and Steidensticker, J. 1993. Behavioral and adrencortical responses to environmental changes in leopard cats (*Felis bengalensis*). Zoo Biology 12**,** 321-331.

Cooper, J. J., and Nicol, C. J. 1991. Stereotypic behavior affects environmental preference in bank voles, *Clethrionomys glareolus*. Animal Behaviour 41**,** 971-977.

Cornin, G. M., Wiepkema, P. R., and van-Ree, J. M. 1986. Endorphines implicated in stereotypies of tethered sows. Experimentia 42**,** 198-199.

Costall, B., and Naylor, R. J. 1975. Actions of dopaminergic agonists on motor function. Advances in Neurology 9**,** 285-297.

Cronin, G. M., and Wiepkema, P. R. 1984. An analysis of stereotyped behaviour in tethered sows. Annals de Recherches Veterinaires 15**,** 263-270.

Dantzer, R., and Normede, P. 1983. De-arousal properties of stereotyped behavior: evidence from pituitary-adrenal correlates in pigs. Applied Animal Ethology 10**,** 233-244.

Duncan, I. J. H., and Wood-Gush, D. G. M. 1972. Thwarting of feeding behavior in the domestic fowl. Animal Behaviour 20**,** 444-451.

Eichler, A. J., Antelman, S. M., and Black, C. K. 1980. Amphetamine stereotypy is not a homogenous phenomenon: sniffing and licking show distinct profiles of sensitization and tolerance. Psychopharmacology 6**,** 287-290.

Eilam, D., and Golani, I. 1994. Amphetamine-induced stereotypy in rats: its morphogenesis in locale space from normal exploration. *In* "Ethology and Pharmacology", in Cooper, S. J. and Hendrie, C. A., Eds.), pp. 241-266. John Wiley & Sons, New York.

Eilam, D., and Szechtman, H. 2005. Psychostimulant-induced behavior as an animal model of obsessive-compulsive disorder: an ethological approach to the form of compulsive rituals. CNS-Spectrum 10**,** 191-202.

Fentress, J. C. 1976. Dynamic boundaries of patternd behavior: interaction and self-organization. *In* "Growing Points in Ethology", pp. 135-167. Cambridge Univesity Press, Cambridge.

Fourie, L. J., and Perrin, M. R. 1987. Social behavior and spatial relationships of the rock hyrax. South Africa Journal of Wildlife Research**,** 91-98.

Fox, M. W. 1965. Environmental factors influencing stereotyped and allelomimetic behavior in animals. Laboratory Animal Care**,** 363-370.

Frank, D., and Dehasse, J. 2003. Differential diagnosis and management of human-directed aggression in cats. Veterinary Clinics of North America - Small Animal Practice 33**,** 269.

Fraser, A. F., and Broom, D. M. 1990. "Farm Animal Behaviour and Welfare." Bailliere Tindall, London.

Gorman, M. L., and Trowbridge, B. J. 1989. The role of odor in the social lives of carnivores. *In* "Carnivore Behavior, Ecology, and Evolution", in Gittleman, J. L., (Ed., pp. 57-88. Chapman and Hall, London.

Hediger, H. 1964. "Wild animals in captivity." Dover, New York.

Henderson, J. G. J., and Pollard, C. A. 1988. Three types of obsessive compulsive disorder in a community sample. Journal of Clincal Psychology 44**,** 747-752.

Henschel, J. R., and Skinner, J. D. 1991. Territorial behavior by a clan of spotted hyaenas *Crocuta crocuta*. Ecology 88**,** 223-235.

Hewson, C. J., Luescher, A. U., Parent, J. M., Conlon, P. D., and R.O., B. 1998. Efficacy of clomipramine in the treatment of canine compulsive disorder. Journal of the American Veterinary Medical Association 213**,** 1760-1766.

Hoeck, H. N., Klein, H., and Hoeck, P. 1982. Flexible organisation in hyrax. Z. Tierpsychol**,** 265-298.

Hutt, C., and Hutt, S. J. 1965. The effects of environmental complexity on the stereotyped behaviour of children. Animal Behaviour 13**,** 1-4.

Immelmann, K., and Beer, C. 1989. "A Dictionary of Ethology." Harvard University Press, London.

Insel, T. 1988. Obsessive-compulsive disorder: new models. Psychopharmacology Bulletine 24**,** 365-369.

Jungius, H. 1971. "The Biology and Behavior of the Reedbuck (*Redunca arundinum*) in the Kruger Nationl Park." Verlag Paul Parey, Hamburg.

Karno, M., Golding, J. M., Sorenson, S. B., and Burnam, M. A. 1988. The epidemiology of obsessive-compulsive disorder in five US communities. Archives of Gen Psychiatry 45**,** 1094-1099.

Kauhala, K., Helle, E., and Taskinen, K. 1993. Home range of the raccoon dog (*Nyctereutes procyonoides*) in southern Finland. Journal of Zoology 231**,** 95-106.

Keiper, R. R. 1970. Causal factors of stereotypies in caged birds. Animal Behaviour 17**,** 114-119.

Lorenz, K. 1952. "King Solomon's Ring: New Light on Animals Ways." Meridian Books (Penguin), New York.

Lorenz, K. 1966. "On agression." Methuen & Co., London.

Luescher, A. U. 2004. Diagnosis and management of compulsive disorders in dogs and cats. Clinical Techniques in Small Animal Practive 19**,** 233-239.

Lyon, M., and Robbins, T. 1975. The action of central nervous system stimulant drugs: A general theory concerning amphetamine effects. *In* "Current developments in psychopharmacology", in W., E. and Valzelli, L., Eds.), Vol. 2, pp. 81-163. Spectrum Publications, New York.

Mason, G. J. 1991. Stereotypies: A critical review. Animal Behaviour 41**,** 1015-1037.

Mason, G. J., and Turner, M. A. 1993. Mechanisms involved in the development and control of stereotypies. *In* "Perspectives in Ethology", in Bateson, P. P. G., Klopfer, P. H., and Thompson, N. S., Eds.), Vol. 10: Behavior and Evolution, pp. 53-85. Plenum Press, New York.

Meyer-Holzapfel, M. 1968. Abnormal behavior in zoo animals. *In* "Abnormal Behavior in Animals", in Fox, M. W., (Ed., pp. 476-503. W.B. Saundares, Philadelphia:.

Moon-Fanelli, A. 2005. Canine compulsive Behavior: An overview and phenotypic description of tail chasing in bull terriers, Vol. 2005.

Muller, K., Hollingsworth, E. M., and Cross, D. R. 1989. Another look at amphetamine-induced stereotyped locomotor activity in rats using a new statistic to measure locomotor stereotypy. Psychopharmacology 97**,** 74-79.

Muller-Schwarze, D. 1972. Social significance of forehead rubbing in blacktailed deer (*Odocoileus columbianus*). Animal Behaviour 20**,** 788-797.

Odberg, F. 1978. Abnormal behaviors (stereotypies). *In* "Proceedings of the 1st World Congress on Ethology Applied to Zootechnics" (Garsi, Ed.), pp. 475-480. Industrias Graficas, Madrid.

Rapoport, J. L. 1989a. The biology of obsessions and compulsions. Scientific American 260**,** 83-89.

Rapoport, J. L. 1989b. "The Boy Who Couldn't Stop Washing: The Experience and Treatment of Obsessive-Compulsive Disorder." E. P. Dutton, New York.

Rasmussen, S., and Eisen, J. L. 1991. Phenomenology of OCD: clinical subtypes, heterogeneity and coexistence. *In* "The Psychobiology of Obsessive-Compulsive Disorder", in Zohar, J., Insel, T., and Rasmussen, S., Eds.), pp. 13-43. Springer Publishing Company, New York.

Rasmussen, S. A., and Eisen, J. L. 1992. The epidemiology and differential diagnosis of obsessive compulsive disorder. Journal of Clincal Psychiatry 53**,** 4-10.

Reed, G. F. 1985. "Obsessional experience and compulsive behaviour: a cognitive-structural approach." Academic Press, Orlando.

Richardson, P. K. R. 1991. Territorial significance of Scent marking during the non-mating season in the *Aardwolf proteles cristatus* (Carnivora: Protelidae). Ethology 87**,** 9-27.

Robbins, T. W. 1977. A critique on the methods available for measurement of spontaneous motor activity. In Eds.),. *In* "Handbook of Psychopharmacology", in Iversen, L. L., Iversen, S. D., and Snyder, S. H., Eds.), Vol. 7, pp. 37-81. Plenum Press, New York.

Robbins, T. W., and Sahakian, B. J. 1981. Behavioural and neurochemical determinants of drug-induced stereotypy. *In* "Metabolic Disorders of the Nervous System", in Clifford, R. F., (Ed., pp. 244-291. Pitman, London.

Rowe-Rowe, D. T. 1992. Survey of south african otters in a freshwater habitat, using sign. South Africa Journal of Wildlife Research 22**,** 49-55.

Rushen, J. 1984. Stereotyped behaviour, adjunctive drinking and the feeding periods of tethered sows. Animal Behaviour 32**,** 1059-1067.

Schenkel, R., and Schenkel-Hulliger, L. 1969. "Ecology and Behavior of the Black Rhinoceros (*Diceros Bicornis L.*)." Verlag Paul Parey, Hamburg.

Schiorring, E. 1971. Amphetamine induced selective stimulation of certain behaviour items with concurrent inhibition of others in an open-field test with rats. Behavioural Brain Research 39**,** 1-16.

Schulte, N., and Klingel, H. 1991. Herd structure, leadership, dominance and site attachment of the camel, *Camellus dromedarius*. Behaviour 118**,** 103-114.

Serruya, D., and Eilam, D. 1996. Stereotypies, compulsions, and normal behavior in the context of motor routines in the rock hyrax (*Procavia capensis*). Psychobiology 24**,** 235-246.

Stevenson, M. F. 1983. The captive environment: Its effect on exploratory and related behavioural responses in wild animals. *In* "Exploration in Animals and Man", in Archer, J. and Birke, L. I. A., Eds.), pp. 176-197. Van Nostrand Reinhold, London.

Szechtman, H., Culver, K., and Eilam, D. 1999. Role of dopamine systems in obsessive-compulsive disorder (OCD): Implications from a novel psychostimulant-induced animal model. Polish Journal of Pharmacology 51**,** 55-61.

Szechtman, H., and Eilam, D. 2004. Animal models in Psychiatry. *In* "The rat: A handbook for the user", in Whishaw, I. Q. and Kolb, B., Eds.). Oxford, New York.

Szechtman, H., Sulis, W., and Eilam, D. 1998. Quinpirole induces compulsive checking behavior in rats: A potential animal model of obsessive-compulsive disorder (OCD). Behavioral Neuroscience 112**,** 1475-1485.

Szechtman, H., and Woody, E. 2004. Obsessive-compulsive disorder as a disturbance of security motivation. Psychological Review 111**,** 111-127.

Terlouw, E. M. C., Lawrence, A. B., and Illius, A. W. 1992. Relationship between amphetamine and environmentally induced stereotypies in pigs. Pharmacology, Biochemistry and Behavior 43**,** 347-355.

von-Uexkull, J. 1957. A stroll through the world of animals and men. *In* "Instinctive Behavior", in Schiller, C. H. and Lashleys, K. S., Eds.), pp. 5-82. International Universities Press Inc, New York.

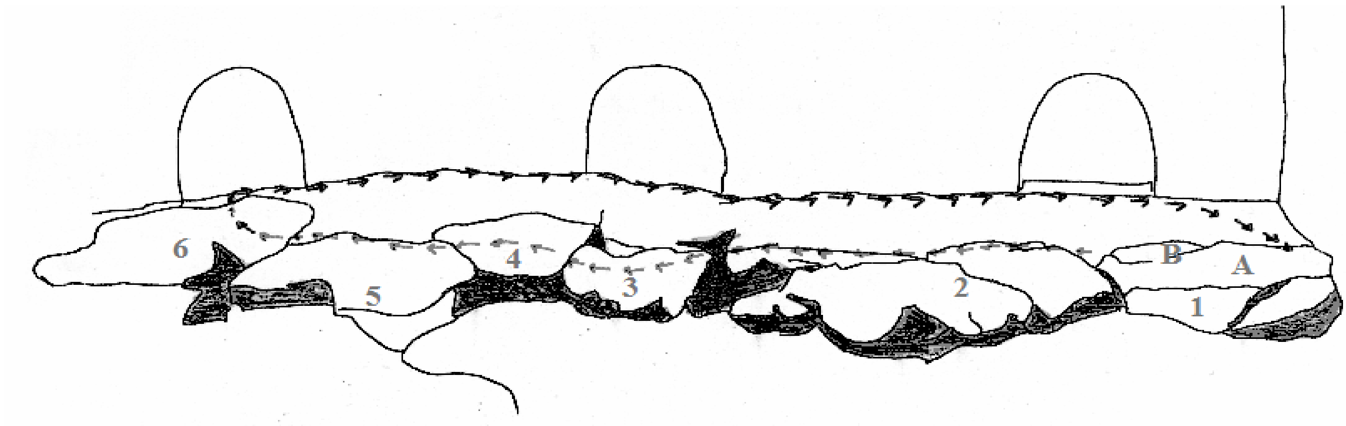
Walther, F. R. 1977. Artiodactyla. *In* "How Animals Communicate", in T.A., S., (Ed., pp. 655-714. Indiana University Press, Bloomington.

Wechsler, B. 1991. Stereotypies in polar bears. Zoo Biology 10**,** 177- 188.

Weissman, M. M., Bland, R. C., Canino, G. J., Greenwald, S., Hwu, H. G., Lee, C. K., Newman, S. C., Oakley-Browne, M. A., Rubio-Stipec, M., and Wickramaratne, P. J. 1994. The cross national epidemiology of obsessive compulsive disorder. The Cross National Collaborative Group. Journal of Clincal Psychiatry 55 (Suppl.)**,** 5-10.

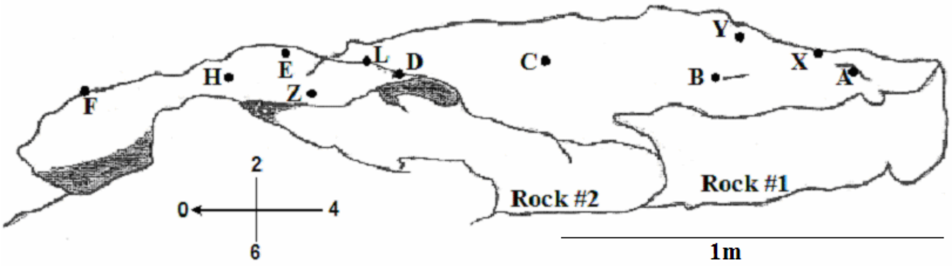
Tables, Figures and their captions

Table 1: The behavior of a black bear during continuous 30 minutes of videotaping comprised 53 repetitions of one stereotyped ritual in which the bear traveled from one rock to another one in a regular path and return in one of four paths to the start point.



#	Ritual	Frequency	Variation	Comments
1	Turns on rock #1	**52**	**1**	Unusual turn on rocks 2-3
2	Turning started with slide hindlegs back, one after the other, followed by flexing the legs and pelvis touch-down	**53**	**0**	
3	Pelvis touch-down occurred either in location A (n=24) or B (40 cm north-east of A; n= 28)	**52**	**1**	
4	While pelvis touched down, head and chest moved to upright posture (while sitting on the pelvis). The forelegs released contact in regular order: first right and then left. Then, trunk rotated clockwise at 180?	**53**	**0**	
5	The forelegs touched down in succession, followed by lowering the head and trunk and then lifting off the pelvis, to bring the trunk to horizontal posture	**53**	**0**	
6	At the horizontal posture, HR was always about 30 cm diagonally ahead of HL	**53**	**0**	
7	Initiating forward progression with HL step	**53**		
8	Progressing along a fixed path, to rocks 2, 3, 4, 5, and 6, and there turning back and returning to rock #1	**37**	**16**	**These took 4 forms, as detailed below** 5 - Turning back on rock #3 5 - Turning back 2 m beyond rock # 6 3 - Turning back 4 m beyond rock # 6 3 - Distracted at rock #5, going around the perimeter back to rock #1
9	Turning clockwise to return to rock #1	**51**	**2**	
10	Four different paths lead back to rock #1, as follows	1) 21		Along the wall back to rock # 1
		2) 13		Parallel to the wall back to rock # 1
		3) 16		Along the central rocks back to rock # 1
		4) 3		Around the perimeter back to rock #1

Table 2: The behavior of a brown bear during continuous 30 minutes of videotaping comprised 92 repetitions of one stereotyped ritual in a specific place, which is the end of a regular path of that bear. The few variations generally occur either when other bears intervene in the ritual, physically blocking the bear from completing the ritual, or when the bear made brief pause to drink water, and then resume the performance of the rituals.

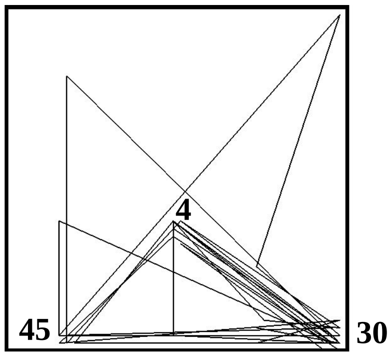


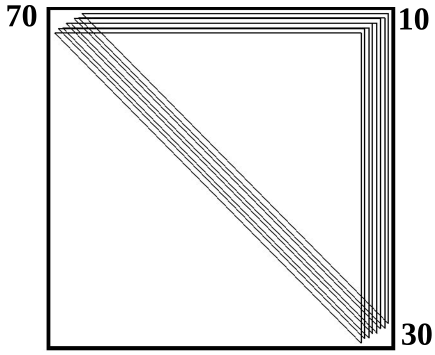
#	Ritual	Frequency	Variation	Comments
1	FR, and then FL, touch down at the edge of rock # 2 at point F	92	0	
2	HR, and then HL, touch down on rock # 2 at point G	92		
3	Head bobbing		46, 25, 21	2,1,0 bobbings, respectively
4	FR extended forward, then flexed backwards, touching down in point H	77	15	FR skipped stretching
5	Clockwise turn	92	0	
6	Initiated forward progression with FR step to point D, followed by FL step to point L, then HL step to point Z, and finally HR step to point D	92	0	
7	FR touched down on point C of rock #1	82	10	FR landed at other locations c rock #1
8	HL touched down in point L on rock # 1 (right after FL liftoff)	92	0	
9	FR touched down in point B on rock #1	90	2	Slight deviation from B
10	FL touched down on point Y of rock #1	89	3	Slight deviation from Y
11	HL touched down on point Y of rock # 1 (right after FL liftoff)	89	3	Slight deviation from Y
12	FR touched down in point X of rock #1, close to the cage wall	92	0	
13	FL touched down at point Z	89	3	Slight deviation from Z
14	Head went up and then down in counterclockwise circular path along the wall	91	1	Counterclockwise head trajectory along the wall
15	HL stepped backwards from point Y to point A	91	1	Deviation from A
16	Counterclockwise turn (or rock # 1, next to the wall)	92	0	
17	FR stepped forward, touching down in point B	92	0	
18	FL touched down in point B	87	5	Slight deviation from B
19	FR made two brief air steps, then touching down in point C	92	0	
20	FL touched down in point C	92	0	
21	FL touched down at point D on the edge of rock # 2	91	1	FR touched down first
22	FR touched down at point E of rock #2	91	1	Consequence of # 21
23	FL step from point D to H (center of rock #2). This was the last step before reaching the edge of the rocks.			

<u>Table 3</u>: Routes and movements in a quinpirole rat (40 min after the 10 injection of 0.5 mg/kg), and an amphetamine rat (32 min after acute injection of 5 mg/kg).

Quinpirole rat	Amphetamine rat

A. Trajectories of locomotion





B. Sequence of stopping places

Quinpirole rat

Time	Start	Stops between			End
40'25"	30	45	4		30
40'33"	30	40	4		30
40'42"	30	4	45	7	30
40'58"	30	45	5		30
41'08"	30	45	1	3	30
41'27"	30	3	4		30
41'37"	30	4			30
41'46"	30	4			30
41'56"	30	35			30
42'05"	30	45	4		30

Amphetamine rat

Time	Start	Stops between		End
32'30"	10	30	70	10
32'42"	10	30	70	
32'54"	10	30	70	
33'04"	10	30	70	
33'15"	10	30	70	
33'26"	10	30	70	
33'38"	10	30	70	
33'50"	10	30	70	
34'02"	10	30	70	
32'30"	10	30	70	

C. Sequence of movements

Time	Movements at place 30
40'25"	V_u V_d C_6
40'33"	V_u V_d C_6
40'42"	V_u V_d C_6 C_2 V_u C_7
40'58"	V_u C_5 A_2 V_u V_d V_u C_6
41'08	V_u A_2 C_6 V_u C_3 V_u C_4 V_d A_3 V_u C_6
41'27"	V_u A_3 C_7
41'37"	V_u V_u A_4 A_2 C_7
41'46"	V_u C_7
41'56"	V_u C_6 A_4 V_d C_3 V_u C_6
42'05	V_u V_d C_4 C_6
40'25"	V_u V_d C_6

Time	Movements at place 10
32'30"	$A_{\frac12}$ C_1 $A_{7\frac12}$
32'42"	$A_{\frac12}$ C_2 A_1
32'54"	A_1 $C_{1\frac12}$ A_1
33'04"	$A_{\frac12}$
33'15'	A_0 C_2 $A_{\frac12}$
33'26"	A_0 C_1 $A_{7\frac12}$ $C_{1\frac12}$ A_1
33'38"	A_0 C_2 A_1
33'50"	$A_{\frac12}$ C_2 $A_{\frac12}$
34'02"	A_0 $C_{1\frac12}$ A_1 $C_{1\frac12}$ $A_{7\frac12}$
32'30"	$A_{\frac12}$ C_1 $A_{7\frac12}$
32'42"	$A_{\frac12}$ C_2 A_1

Time	Movements at place 4
40'25"	Circling around object
40'33"	Circling around object
40'42"	Circling around object A_0 V_u A_3
40'58"	Circling around object
41'08	Passing by without stop
41'27"	C_2
41'37"	Circling around object
41'46"	Circling around object
41'56"	C_2 A_6 V_u V_d C_2 V_u
42'05	Skipping that location
40'25"	V_u C_3

Time	Movements at place 70
32'30"	C_0
32'42"	C_0 $A6_{\frac12}$ C_0 A_7
32'54"	$C_{0\frac12}$
33'04"	$C_{7\frac12}$ $A_{6\frac12}$ $C_{7\frac12}$
33'15'	A_6 C_0 $A_{6\frac12}$
33'26"	A_6
33'38"	$A_{6\frac12}$ $C_{7\frac12}$ A_7 A_6
33'50"	A_6 C_0 A_6
34'02"	$A_{6\frac12}$
32'30"	C_0
32'42"	C_0 $A6_{\frac12}$ C_0 A_7

Table 4: A comparison of the characteristics of behavior of rats treated chronically with quinpirole (10 injections of 0.5 mg/kg; based on data from Szechtman et al., 1998 and Ben-Pazi et al., 2001), and rats under acute injection of amphetamine (5mg/kg; based on data from Eilam and Golani 1994).

Quinpirole rats	Amphetamine rats
1. Increased activity (= traveling greater distance)	
2. Increased path stereotypy (= traveling repeatedly the same few paths)	
3. Increase in stopping at the same few places, but decrease in the number of stopping places	
4. Each stopping place has a typical and specific ritual (= behavior differs among places)	4. Behavior looks similar at various stopping places (due to elimination of certain movements)
5. Decreased repetition of movements at specific places	5. Increased repetition of movements at specific places
6. Flexible routes	6. Rigid routes
<u>**Summary**</u> **Stereotyped performance arises from change in the spatiotemporal organization, but not in the content of behavior**	<u>**Summary**</u> **Stereotyped performance arises from change in the content of behavior, by eliminating certain movements and repeating the remaining movements**

Table 5: A ritual of locking a car by OCD patient. The ritual comprised two phases: (a) inside the car; and (b) outside the car. When outside the car, the OCD patient circled around the car whereas the control just locked the door and walked away. Performing this ritual took the OCD patient 215 sec compared with 17 sec of the control person (meaning that the OCD ritual was 12 fold longer). Table 5a

(a) - Inside the car

I. OCD PATIENT

Location/object

Ignition key	Light switch	Steering wheel	Gear stick	Other actions
Switch engine off				
Take out the key	Switch on and off			
	Switch on and off			
	Switch on and off			
Inset in the key				
Switch on and off		Hold it		
			Lock it	
			Move it forth and back	
			Move it forth and back	
			Move it forth and back	
			Move it forth and back	
			Press it down	
			Move it forth and back	
			Move it forth and back	
		Rotate left		
			Press it	
			Move it forth and back	
			Move it forth and back	Collect hand bag
		Rotate right		
Switch on and off				
Take out the key				
		Rotate right		
		Rotate left		
	Switch on and off			
			Move it forth and back	
			Press it	Get out from the car
Total acts:				
6	*4*	*5*	*13*	*2*

II. CONTROL PERSON

Location/object

Ignition key	Lights	Steering wheel	Gear stick	Other actions
Switch off				
Take out the key			Lock it	Get out from the car
Total acts:				
2	*0*	*0*	*1*	*1*

(b) - Outside the car

I. OCD PATIENT

Location/object

Door handle	Door window	Side mirror	Antenna	Other activities
Lock FL				
Check FL		Fold FL	Insert antenna	
		Check FL		Place hand bag on car roof
Check FL		Check FL	Check Antenna	
	Check FL			
Check FL	Check FL			
Check HL				
	Check HR			
Check HR				
Check FR	Check FR	Fold FR	Check antenna	
		Check FL		
Check FL	Check FL			
Check HL	Check HL			
Check rear				
Check HL				Take hand back and walk away
Total acts:				
11	*6*	*5*	*3*	*2*

II. CONTROL PERSON

Location/object

Door handle	Door window	Side mirror	Antenna	Other activities
Lock FL				Get out from the car
Check FL				
Total acts:				
2	*0*	*0*	*0*	*1*

<u>Table 6</u>: Four repetitions of a ritual of blowing and wiping the nose in an OCD patient. There is relatively low variability, mainly in lateral movements. The beginning of the third repetition was missing in our video records, and there is a sudden variation after *Blow* in repetition 2, where cleaning shirt and hands also appears between *Blow* and *Wipe* rather than only after *Wipe*. Otherwise, similar sequential structure is apparent. The duration of each ritual was almost 4 minutes, comprising altogether 20% of the hour of observation (Table based on Szechtman, H. and Eilam, D. Psychiatric models. In: I.Q. Whishaw and B. Kolb (eds.), *The Behavior of the Laboratory Rat: A Handbook with Tests*. London: Oxford University Press (2004); pp 462-474.

Repeat	*Act*	Taking a tissue paper	Blowing or wiping the nose and/or mouth	Handling the used tissue paper
1	*Blow:*	H C Pr F Ra	Pl **W_1** x 4 S	Rc Pu
	Wipe:	H C Pr F Rc Ra	Pl **W_2** S	Fo
			Pl **W_3** x 4 S	Ra Rc F
			Pl **W_4** x 4 S	Rc F Pu Cleaning shirt and hands
2	*Blow:*	H C Pr F Ra	Pl **W_1** x 4 S	Rc F Ra F Pu Cleaning shirt and hands
	Wipe:	H C Pr F Rc Ra	Pl **W_2** x 2 S	Fo
			Pl **W_3** x 4 S	Rc Rc F
			Pl **W_4** x 4 S	F Pu Cleaning shirt and hands
3	*Blow:*	*Missing on tape*		
	Wipe:	H C Pr F Ra Rc	Pl **W_2** x 4 S	Fo
			Pl **W_3** x 4 S	Rc Rc F
			Pl **W_4** x 4 S	F Pu Cleaning shirt and hands
4	*Blow:*	H C Pr F Ra	Pl **W_1** S	Rc Ra F Pu
	Wipe:	H C Pr F Ra Rc	Pl **W_2** x 2 S	Fo
			Pl **W_3** x 4 S	Rc Ra F
			Pl **W_4** x 2 S	F Pu Cleaning shirt and hands

Legend:

Blow – refers to the entire first row in each repetition and is a label for taking a piece of tissue paper, blowing the nose, and putting the tissue down.

Wipe – refers to the remaining rows in each repetition and is a label for taking a piece of tissue paper, wiping the nose, upper lips and under the nose, and putting the tissue down.

H - Holding horizontally in the left hand the roll of tissue paper.

C - Turning the roll so that two pieces of tissue hang down, holding them between the thumb and the other 4 fingers, and detaching the two pieces. The act takes place with what appears to be high concentration, with the eyes following every movement being performed.

Pr - Placing the tissue roll back on the dresser, with the left hand.

F - Holding vertically the tissue piece and folding it along a line perpendicular to the ground, and then smoothing the fold with two fingers from top to bottom.

Fo - Flipping over the folded piece of tissue.

Rc, Ra - Rotating the piece of the tissue by 90? clockwise (Rc) or anticlockwise (Ra).

Pl - Placing the piece of tissue on the body part to be wiped. The tissue covers the nose and the mouth, is held first with only one finger, and then by four fingers at each side.

W_1 - Blowing the nose strongly after a deep breadth and blowing the air intensely so that two holes are formed in the tissue. Piping movements occur in the fingers starting with the median and ending with the lateral fingers.

W_2 - Wiping the upper lip while moving the head to the right and opening the mouth, and then wiping the lower lip while moving the head to the left and closing the mouth.

W_3 - Wiping the nose while moving the head up and down.

W_4 - Wiping under the nose while moving the head up and down with closed eyes.

S - Staring at the tissue with high concentration for several seconds.

Pu - Placing the used piece of tissue, with the left hand, on top of the previously used tissues.

x2 or **x4** – two or four repetitions, respectively.

<u>Figure 1</u>

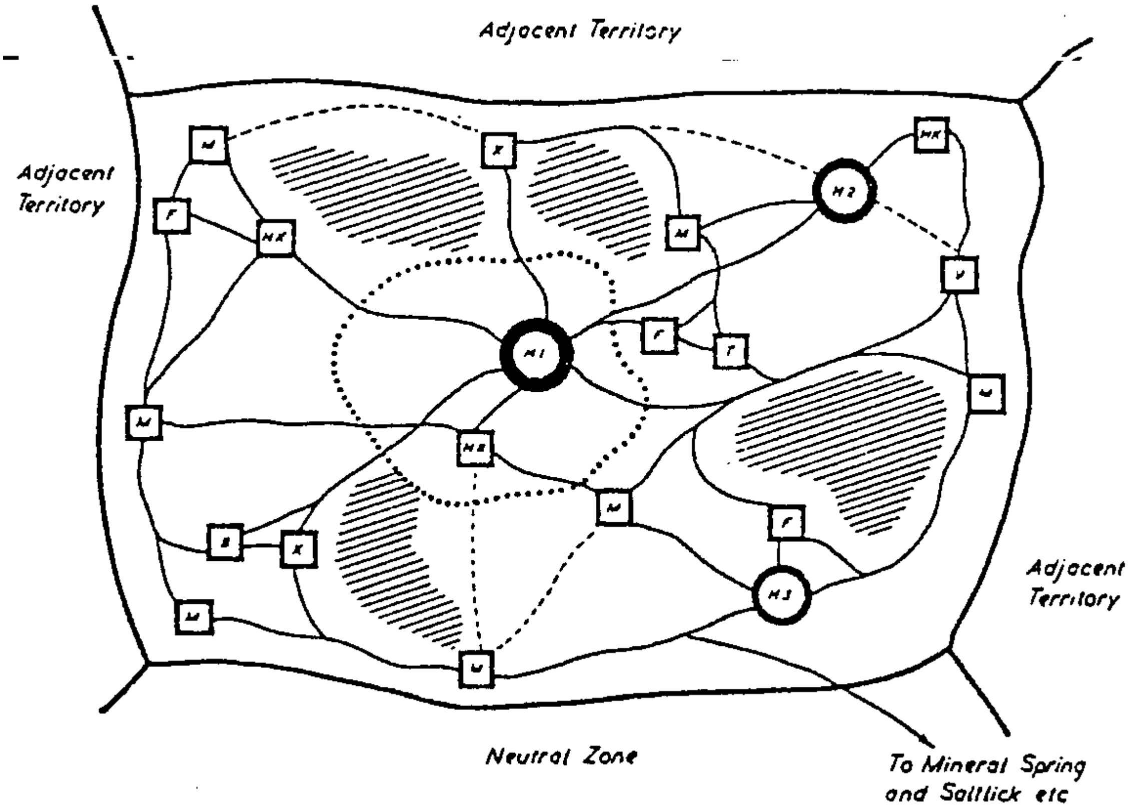
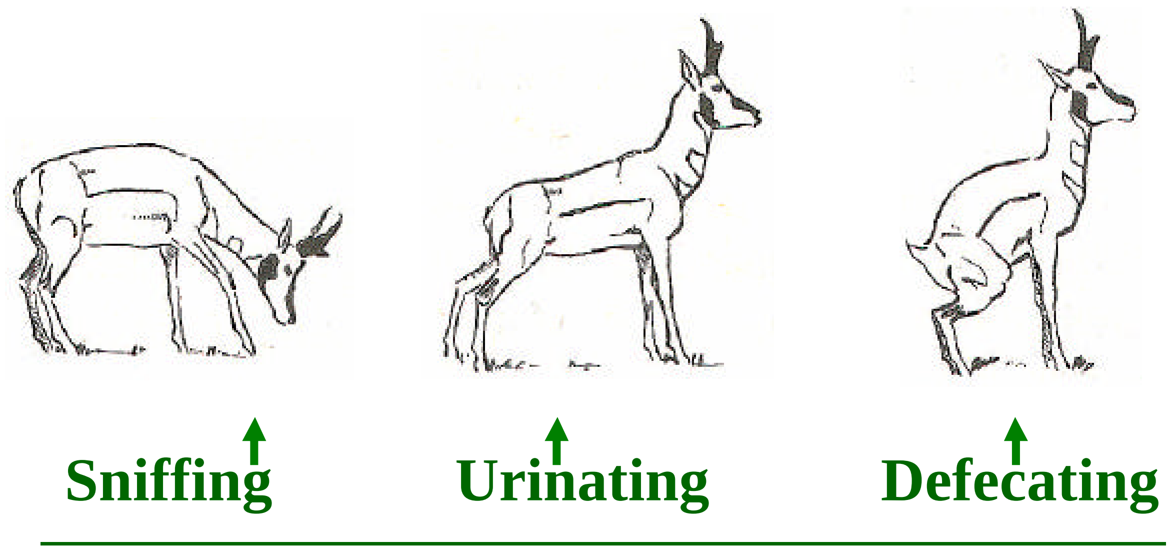


Figure 5. A Territory

- *H1* — *Home 1, maximum (relative) concealment*
- *H2* — *Home 2, refuge*
- *H3* — *Home 3, emergency cover*
- *B* — *Bathing places*
- *F* — *Feeding places*
- *K* — *Places for excretion*
- *HK* — *Urinating and defaecating places*
- *M* — *Demarcation points*
- *T* — *Drinking places*
- *V* — *Food stores*

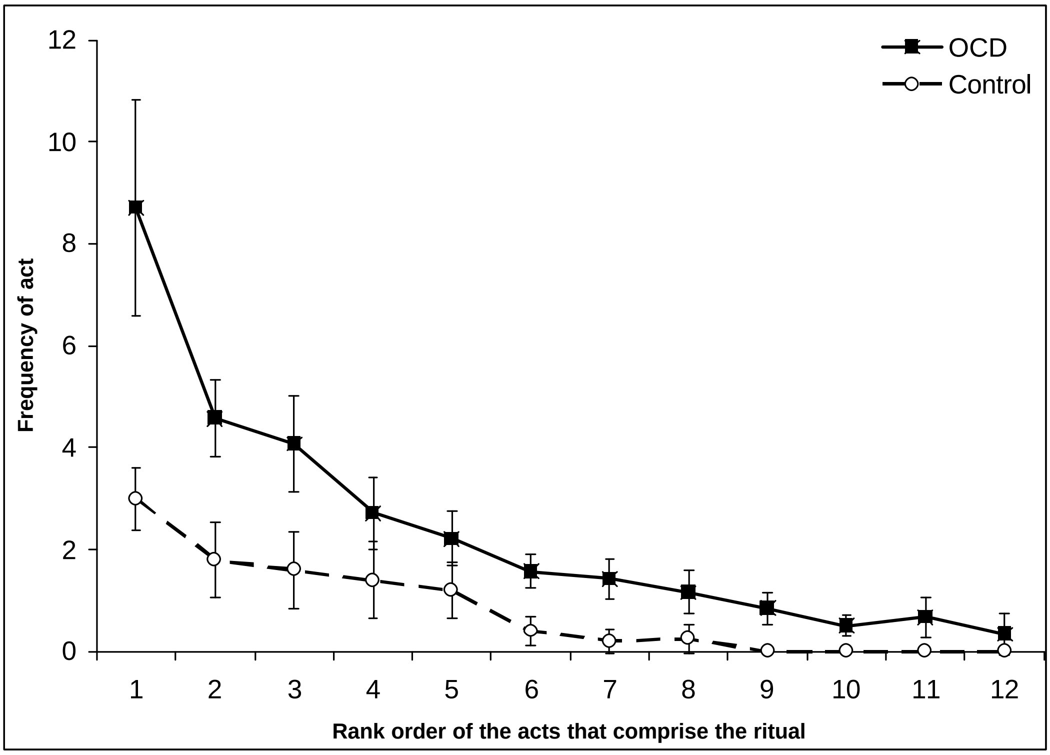
The structure of territory, as proposed by Hediger (1964). The territory comprise three home locations (marked by circles), another set of locations, each with a typical behavior (marked by squares), and a network of routes (marked by lines) that connect these locations.

Figure 2



A demarcation ritual of pronghorn (from Walther, 1977). The pronghorn arrives at the demarcation locale, and first sniffs the ground while gently punting and rubbing it with a foreleg. Then it steps forward with only the forelegs while hindlegs are rooted. As a result the trunk is stretched forward and the antelope urinates in the center of the demarcation place. The pronghorn then steps forward with the hindlegs while the forelegs are rooted. As a result the trunk is arched and the pronghorn defecates in the center of the demarcation place.

Figure 3



Frequency of the acts that comprise rituals. For each ritual, the frequency of acts at each location were counted and sorted from high to low. The mean (±SEM) of each rank was then calculated and depicted in the figure for OCD patients (■) and their controls (?).