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The Dynamics of Brain Activity During Adaptation to Restrictions of External Performance of an Element of Individual Experience

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Abstract

Introduction. This study concentrates on changes in individual experience when the external performance of one of its elements – namely, the system that is formed during learning this behavioral act – becomes impossible. The circumstances entailing inability to perform the behavior that have previously helped to achieve results are considered as ‘restriction’. The primary objective of this study was to identify possible modifications in the structure of individual experience when one of its elements cannot be performed, which is reflected in changes in the characteristics of neural activity.

Methods. Neuronal activity in rat cortex was recorded during restricted food-seeking instrumental behaviors, when we removed the pedal in one side of the cage, which was previously associated with feeding. In order to determine the patterns of neuronal activity and to analyze its dynamics we recorded it before restriction of definitive behavior, and after restriction in the opposite side of the cage when the pedal was not removed.

Results. Compared to definitive behavior, changes in neuronal activity in terms of restriction are mainly associated with the loss of the ability to perform behaviors leading to goal achievement. The results speak in favor of neurons that were activated in preserved behavior and changed their activity in terms of restriction (which was possible both before and during restriction).

Discussion. The findings confirm modifications in the structure of individual experience associated with restrictions of external performance of one of its elements that affect not only the restricted element of experience, but also the elements associated with it. Experiments aimed at identifying mechanisms influencing memory in animals are important for understanding the dynamics of human memory, as well as for developing approaches to its ‘editing’ in clinical practice.

Keywords
individual experience, neuron activity, behavior, restrictions of performance, adaptation, inconsistency, learning, reconsolidation modification, element of experience, instrumental extinction

Highlights

► Restrictions of 'external' performance of an element of individual experience involves modifications in its structure, which is accompanied with changes in the dynamics of brain activity.

► Changes in the structure of individual experience affect not only an element of experience, which 'external' performing is directly subjected to restriction, but also other related elements.

► Events entailing the impossibility of 'external' performance of an element of experience change the characteristics of animal behavior.

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Introduction

The present study attempts to investigate the changes in individual experience when the 'external' performance of one of its elements becomes impossible. In contrast to the 'internal' performance of an element, the 'external' one means the implementation of this act in the external environment, which leads to the achievement of the result of this act. A system-evolutionary approach in psychophysiology underlay the methodology of this study (Shvyrkov, 1995; Aleksandrov, et al., 1997). Within the system-evolutionary approach, the concept of 'individual experience' – the main subject of psychology – is applied to a structure which can be empirically studied using certain methodological techniques (Ponomarev, 1983; Aleksandrov, 2006). The concept of 'individual experience' describes a psychological structure representing an assembly of models of individuals' interaction with the environment and providing a fixation and reproduction of certain interactions.

The elements that constitute individual experience are functional systems (Anokhin, 1975). In each new episode of learning individuals acquire a new element of experience that joins the already existing structure. The functional system of a behavioral act (an element of experience) is associated with a certain group of specialized neurons (Shvyrkov, 1995). The specialization of neurons is expressed in their absolute activation when individuals perform certain behavioral acts. The systemic specialization of the neuron is largely determined by the genetic program and is constant (Shvyrkov, 1995; Aleksandrov, 2005).

Thus, the formation of a new element of experience is associated with the acquisition of systemic specialization by a group of neurons. The acquisition of new neural specializations starts with a situation of inconsistency, when the available result does not satisfy the needs of the organism and the existing behavior models fail to solve actual problems (Aleksandrov, 2005). Novel events contribute to significant increases in expressions of early genes (the c-fos gene, in particular), representing an initial stage of the cascade of molecular biological changes in neurons (Anokhin, 1997). The c-fos expression is one of the inconsistency markers. The neurons acquiring their systemic specialization are selected from cells with c-fos expression (Svarnik, Anokhin, & Aleksandrov, 2001). At the behavioral level, individuals seek to eliminate situations of inconsistency by searching for solutions to problem situations through generating trial implementations of new behaviors. Achieving a useful result is a criterion for individuals' successful acquisition of new experience. In this case, a new element of individual experience is formed. This newly formed element joins the general structure; previously formed experience undergoes changes (Aleksandrov, 2005). The findings of numerous studies confirm the role of new elements of individual experience (McKenzie, Robinson, Herrera, Churchill, & Eichenbaum, 2013).

Some events make it impossible to find new ways to achieve a previous result. At that point, adaptation to new conditions (possibly due to modifications in the relations between elements of experience) becomes the only way to eliminate the inconsistency between needs and possibilities of achieving results. The concept of restriction embodies all the events that entail the impossibility of performing behaviors that previously led to the achievement of important results (due to the elimination of the object of interaction).We assume that the experience of adapting to restriction changes individual experience. This study aims to elucidate the characteristics of these changes in the structure of animal experience under restriction.

Currently, the studies on the extinction of instrumental skills are the most phenomenologically relevant to the problem of adapting to the impossibility of performing learned behavior. The studies on instrumental 'extinction' are based on the 'stimulus-response' methodology, which is different from the system-evolutionary methodology (Shvyrkov, 1995; Aleksandrov, 2005; *Alexandrov, 2018*). However, these studies address similar issues. In these works, researchers examine whether adaptation to the situation of the impossibility of performing the learned skills can be considered as learning, or it is rather the elimination of old inefficient models (Trask, Thrailkill, & Bouton, 2017; Todd, Vurbic, Bouton, 2014; Bouton, Trask, & Carranza-Jasso, 2016). Learning extinction is defined as process of acquiring a failure predicting skill.

Adaptation to such an undesirable situation as the impossibility of external performance of experience and the termination of inconsistency may be a result that replaces the previous result. Modification changes probably occur as an option, without acquiring a new element of experience, due to reconsolidation changes in associations among the already existing elements of experience.

The present study addresses expected changes in the structure of individual experience when the external performance of one of its elements is impossible. To investigate this issue, an attempt will now be made to identify and describe the behavioral characteristics and dynamics of neural activity during adaptation in terms of restriction.

We hypothesize that neurons that are active in previous experience may change their activity characteristics. Moreover, we assume that neurons associated with the preservation of behavior may also change their activity. In other words, neurons that are activated in certain behavioral act before and after restriction change their activity in terms of restriction.

Methods

The study was conducted on 7 adult Long-Evans rats (weight range 200 to 350 g). The animals were food-deprived during experimental sessions and trainings; weight loss was no more than 15% of their body weight. The experiments were performed in accordance with European Directive 86/609/EEC/11.24.1986 regulating the use of animals for experimental and other scientific purposes.

All the experiments were carried out in a special two-section cage (Fig. 1) bisected by a partition and equipped with photoelectric sensors for behavior control. The opposite angles (sides) of each section of the cage contained two feeders and two pedals. The feeders were placed at farthest corners of the cage, while the pedals were at the nearest ones. When the animals pressed the pedal, a special food tablet was automatically thrown into the feeder; the experimenter could also feed the tablet to the feeder by pressing a button.

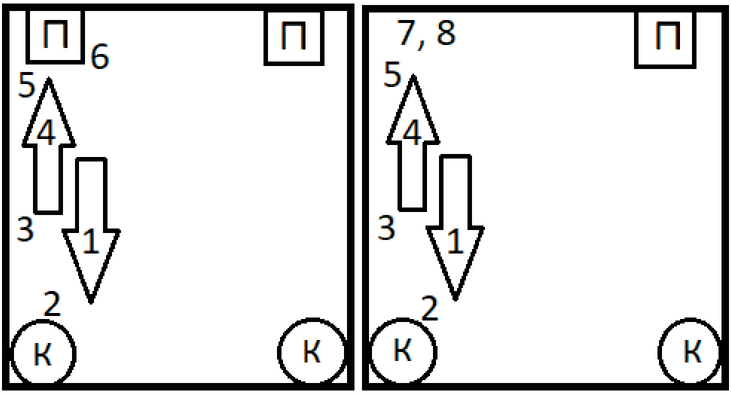


Figure 1.The experimental cage sections with 2 pedals (P) and 2 feeders (F)

Acts of instrumental food-seeking behavior: 1 – approaching the feeder; 2 – immersing the muzzle into the feeder; 3 – moving away from the feeder and approaching the pedal; 4 – passage through a partition; 5 – staying in the corner equipped with the pedal; 6 – pressing the pedal; as well as acts specific to restriction: 7 – sniffing the walls around the pedal; 8 – sniffing the holes in place of the removed pedal

Before the experiment sessions recording neural activity, we have carried out preliminary phased training in instrumental food-seeking behavior in rats. Within this training, we trained rats in food-seeking behavior at one side (pedal-feeder) of the cage. The training process was divided into 6 phases: approaching the feeder; immersing the muzzle into the feeder; moving away from the feeder and approaching the pedal; passing the partition; staying in the corner equipped with the pedal; pressing the pedal. During training sessions, the animals made 50-100 successful reinforced realizations of the corresponding acts of instrumental behavior. Certain acts (Fig. 1) constitute a cycle of instrumental food-seeking behavior (CIFB). Special attention was devoted to a specific act of food-seeking behavior – test immersing the muzzle into the feeder. An animal was considered to have learned behavior pattern if it performed independently more than 20 full cycles of instrumental food-seeking behavior.

After training we kept the animal in its home cage at rest for several days without restriction in food. The implantation of microelectrodes was then carried out under general anesthesia (Zoletil, Rometar). We scalped the animals, then trepanned them and installed manipulators above the place of registration of impulse activity corresponding to the localization of the retrosplenial cortex of the rat brain (P 5.0; L 0.5) (Paxinos, & Watson, 1997). Further, we lowered microelectrodes into the brain. We chose retrosplenial cortex to record neuronal activity. This could increase the likelihood of recording the activity of neurons specialized in instrumental food-seeking behavior based on previous studies (Gorkin, Kuzina, Ivlieva, Solovyova, & Aleksandrov, 2017; Kuzina, Gorkin, & Aleksandrov, 2015; Shevchenko, Aleksandrov, Gavrilov, Gorkin, & Grinchenko, 1986).

During the experiment, impulse signal from the electrodes passed through a signal amplifier (gain 3000, bandwidth 100 Hz – 2 kHz) (Gorkin, 2011), and then it was sent to the computer device, where the Discovery program (DataWaveTechnologies, USA) was used to record data from the tetrode. Besides, we used the photoelectric method to record the behavioral marks of pedal pressing, passing the partition and immersing the muzzle into the feeder. Thus, both spike activity of neurons and reference marks of behavior were recorded by the Discovery in a single file, with a single reference point, which allowed us to accurately compare individuals' behavior with their neural activity.

Further, we recorded the activity of retrosplenial cortical neurons in the behavioral cycles of animal food seeking on the side of the cage where the training took place. Then the experimenter turned off the working pedal, which pressing became ineffective. At that moment, we turned on the second pedal (on the other side of the cage); the animal had to learn how to press it. After training (the criterion was an average of 20 pressures), the experimenter switched the effectiveness of pedals; the first one became effective again, and so on (20 pressures for each pedal). After several sessions of pressing both pedals in turn, we removed the first one from the cage; a hole remained in its place, while the second pedal was untouched and remained in the 'alternating efficiency' mode (ineffective when we removed the first pedal). Thus, the animal found itself in a situation of impossibility to implement behavior – restriction. The animal stayed in terms of restriction for 5 minutes (average implementation time of 20 successful food-seeking behavioral act), after which another pedal became effective. After 20 successful pressures of the 'preserved pedal, the experimenter turned off its effectiveness. The animal was in terms of restriction again. In each session, we registered 2-3 restrictions alternating with successful behaviors on the other side of the cage. During all the experimental sessions, we recorded videos of the behavior of the animals and all the key moments of the sessions.

We distinguished the recorded multicellular activity from artifact signals and then divided them into separate clusters according to the signal amplitude at different electrodes. The resulting activity of individual neurons was compared with the behavior of individuals using the NeuRu program (A.K. Krylov). On the side of the cage, where we restricted the implementation of the behavioral act, we identified certain acts of food-seeking behavior, orientation, grooming and other forms of behavior as well as modified acts of behavior.

We were interested in the activity of neurons specialized in the behavioral acts identified by us (the 100% probability of activation in a particular act corresponds to 'specific' activity), as well as the neurons with not determined specialization but which were active in instrumental food-seeking behavior. If it was impossible to establish the association between the activation of a neuron and certain acts of behavior, or if activation of a neuron was not observed in the studied food-seeking behavior, we considered such cells as 'nonspecifically active'. In other words, they were considered as specialized in other forms of behavior formed irrespectively our trainings (Aleksandrov et al., 2014). Among these cells we distinguished those ones the probability of activating which reached more than 40–50% during the performance of one or more successive acts. We suggest that such neurons may be specialized in other behaviors, but are indirectly involved in ensuring the realization of this food-seeking behavior. Thus, for further statistical analysis we selected all the cells the probability of activating which was above 50%; we analyzed specialized cells additionally.

Using the NeuRu program, we obtained the activation frequency of individual cells for each implementation of behavioral acts. We carried out a statistical comparison between activation frequencies in acts of a successful food-seeking behavior before restriction and the acts of behavior when it was impossible to implement instrumental food-seeking behavior according to the Wilcoxon criterion; after obtaining significant differences, we analyzed the direction of changes. Similarly, we carried out a statistical comparison by food-seeking behavior at the other side of the experimental cage before and after restriction ("preserved" behavior) and for acts of other behaviors.

Results

The experiment with registration of neural activity was conducted on 7 adult Long-Evans rats. For some animals (4 rats), after a long restriction (several days, and accordingly, experimental sessions) we held a 'return' session – returning the previously removed pedal and reactivating its effectiveness. Further, 2 animals were subjected to restriction, when the second pedal was removed from the experimental cage.

The existing knowledge of the behavior of different animals in terms of prohobition enabled us to identify the most common specific acts that that were associated with the modified ineffective instrumental food-seeking behavior: approaching the hole in place of the removed pedal, finding the removed pedal in the corner, sniffing the hole, sniffing the corner in place of the removed pedal, approaching the feeder, immersing the muzzle into the feeder, passage through a partition (Chistova, Ivlieva, & Gorkin, 2018).

These behavioral acts could be compared with the acts of successful instrumental behavior. They were either similar to the acts of successful food-seeking behavior, or took place in the same place of the experimental cage. When comparing behavior parameters and neural activity we examined only the acts which were performed 3 times at least. We should note that in terms of restriction animals performed a fragmented cycle of instrumental food-seeking behavior; for example, after finding the pedal in the corner of the cage, they extremely rarely approach to the feeders. This indirectly indicates that changes occur when it is impossible to perform an element of individual experience in the integral structure of experience.

During the restriction sessions, we observed other forms of behavior including acts of grooming, which were predominantly performed by the animal near the hole in place of the removed pedal, and acts of orienting and exploring behavior (standings, sniffing of the cage). We observed a general decrease in the frequency of performing food-seeking behavior in terms of restriction (Mann–Whitney test, p <0.05), a decrease in the duration of these performances (Mann–Whitney test, p <0.05), and also a change in the ratio of the number of performed food-seeking behaviors and other forms of behavior (see Fig. 2).

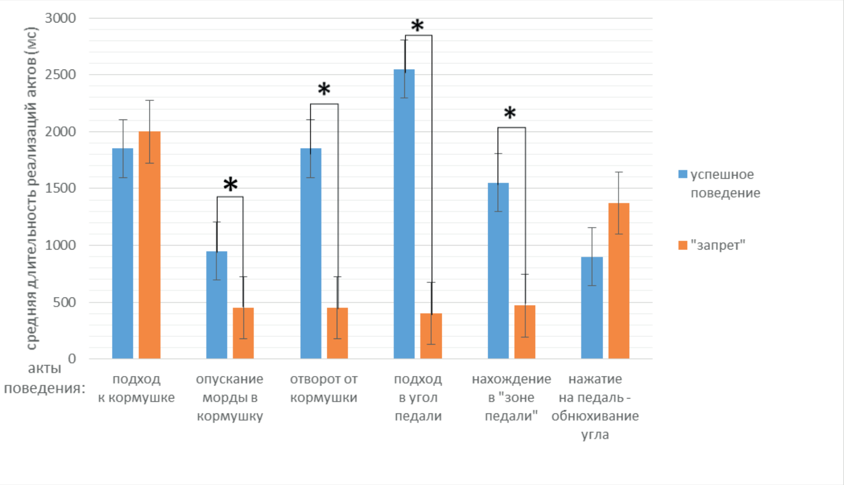


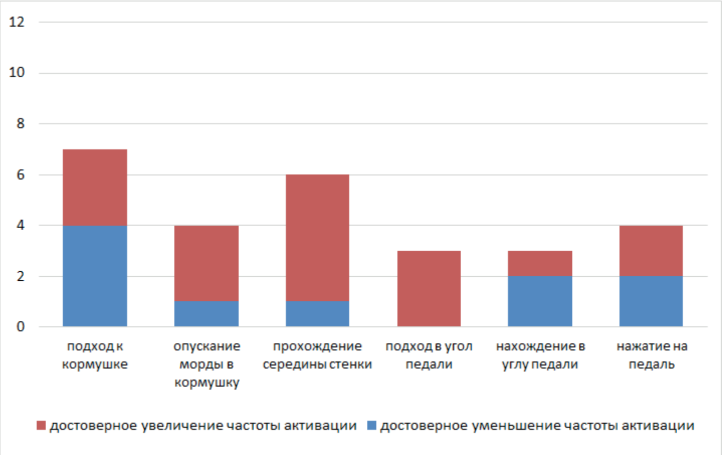
Figure 2. Comparing the average durations (ms) of performing successful food-seeking (in blue colour) and modified acts after removing the pedal (in orange colour)

Values represent the means ± standard errors. Asterisks indicate significant differences by the Mann–Whitney test (p < 0.05)

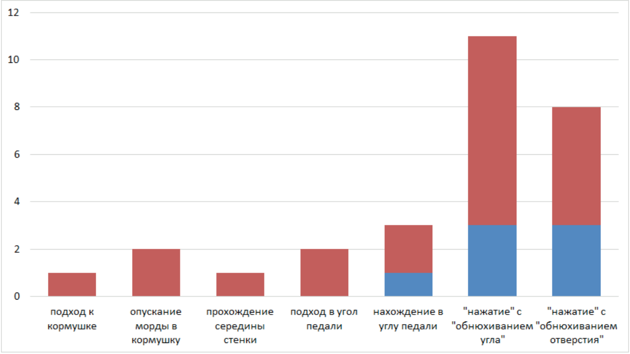
According to the Mann-Whitney criterion, the frequency of acts of orientating and exploring behavior (standings) turned out to be less significantly less ($p < 0.05$) in definitive behavior (the frequency of performing acts was 0.60 ± 0.15per minute) than in terms of restriction (frequency of performing acts was 0.15 ± 0.05). Meanwhile, the mean time for performing such acts in terms of restriction has not changed. Besides, after restriction the frequency and average duration of grooming acts did not change.

To control the changelessness of the position of the recording electrodes, we compared the activity of a population of neurons recorded from an individual animal's cortex before and after the procedure of pedal removing during the performance of various forms of behavior in that part of the experimental cage where the animal was placed at the beginning and the end of the experimental session. After comparing the general population activity using the Wilcoxon statistical criterion, in 7of 9 cases (restriction session) the average frequency of the activity of neuronal population did not significantly change ($p > 0.05$); 2 cases of a significant decrease in general population activity were excluded from the comparative analysis of neural activity in terms of restriction.

In the recorded multicellular activity we distinguished 30 patterns of activity of individual neurons. Meanwhile, we observed no specialized acts of food-seeking behavior in the experimental cage. We analyzed the activity of registered neurons during the performance of modified acts in terms of restriction. The number of acts performed was insufficient for the act-by-act statistical comparison in one animal (for 4 neurons). The analysis of the average frequency of neuronal activity, when the animal subjected to restriction, did not reveal significant changes compared with the activity of neurons during the performance of definitive behavior. The act-by-act statistical comparison showed that 15 of 26 neurons significantly changed the frequency of activity in at least a single act in terms of restriction (Fig. 3) (Mann-Whitney test, $p < 0.05$). Moreover, the greatest number of changes was observed in the following pairs of compared acts: successful pedal pressing / sniffing the walls in place of the removed pedal; successful pedal pressing / sniffing the holes in the removed pedal (11 and 8, respectively). All significant changes in the frequency of impulse activity were unidirectional in the context of belonging to a single neuron. In other words, the frequency of activity of an individual neuron either decreased or increased, with the decrease in the frequency of activity observing only in acts associated with the pedal removed ('approaching the corner', 'sniffing the corner', and 'sniffing holes').



(a)



(b)

Figure 3. Histograms of the number of neural activity patterns with a significant change in the frequency of activity in terms of prohibition

Distribution of the number of significant differences in the activity of individual neurons in the acts of:
(a) The food-seeking cycle preserved its efficiency: approaching the feeder – 7 neurons; immersing the muzzle into the feeder – 4 neurons; passage through a partition – 6 neurons; finding the pedal in the corner – 3 neurons; pressing the pedal – 4 neurons.
(b) The modified food-seeking behavior: approaching the feeder – 1 neuron; immersing the muzzle into the feeder – 2 neurons; passage through a partition wall – 1 neuron; approaching the pedal – 2 neurons; finding the pedal in the corner – 3 neurons.
Comparing the frequency of activity in 'pressing the pedal' and 'sniffing the corner in the zone of the pedal' – 11 neurons.
Comparing the frequency of activity in 'pressing the pedal' and 'sniffing the holes' – 8 neurons.

We discovered the neurons that were active in behavior in the part of the cage not subjected to restriction (in preserved behavior); these neurons changed their activity in terms of restriction. A more detailed analysis of the "preserved" instrumental food-seeking behavior was carried out for individual neural activity patterns. The act-by-act statistical comparison (the Mann–Whitney criterion) showed that the frequency of activity of 14 neurons during the performance of "preserved" behavior did not significantly change after the animal was subjected to restriction ($p > 0.05$). We observed significant changes in individual acts of behavior preserved its effectiveness in the activity of 16 neurons($p < 0.05$): in approaching the feeder – 7 neurons; immersing the muzzle into the feeder – 4 neurons; passage through a partition – 6 neurons; approaching the pedal – 3 neurons; finding the pedal in the corner – 3 neurons; pressing the pedal – 4 neurons. Significant changes in the frequencies of neuronal activity in the acts of preserved behavior (compared to these acts before restriction were multidirectional in the general population, exhibiting both the increase and the decrease in frequencies (Fig. 3). However in 15 of 16 neurons the frequency of activity of individual cells changed unidirectionally.

Thus, we may argue that restriction of on the performance the behavioral cycle in one part of the cage changes neuronal activity during the implementation of the behavior that has preserved its effectiveness. We now may assume that in this situation the greatest changes in the structure of individual experience are associated with the expectation of a result at the stage that immediately precedes the consummate act.

Discussion

In the experiments, we observed significant changes in the activity of neurons, which speaks in favor of modifications in the structure of individual experience, associated with the impossibility of "external" performance of one of its elements.

We found multidirectional significant differences in the frequency of activity of neurons during animals' performance of acts in the 'pedal zone' before and after its removal. The most part of the neurons that changed their activity in the restricted side increased the frequency of activation. The neurons that decreased their activity also showed a very low frequency before restriction. The decrease in their activity may be explained by the lack of behavior in which these cells showed non-specific activation. For the most part of cells the increase in the frequency of activity that changed their activity in the 'pedal zone' is presumably associated with inconsistency and the attempts to eliminate it. We also observed an increase in the number of standings in terms of restriction compared with the sessions of definitive behavior. As an indicator of orientating and exploring behavior standings may indicate a prolonged inconsistency experienced by the individual in terms of restriction. We assume that if trial acts and food-seeking behavior do not lead to finding new ways to achieve a result, inconsistency is prolonged. This prolonged inconsistency does not eliminate the contradiction between the metabolic 'needs' of the neuron and the real environment; death genes can be expressed in neurons, which lead to programmed cell death – apoptosis of neurons (Aleksandrov, 2004). Neuron death is a necessary condition for the formation of individual experience "when the metabolic needs of a neuron come into fatal contradiction with new ways of coordinating the needs of individual cells" (Aleksandrov, 2005, p. 853–855). In terms of restriction some cells with the increased activity may subsequently undergo apoptosis as part of general changes in the structure of experiment.

We discovered that the neurons that were nonspecifically activated in the 'preserved behavior' changed their activity (compared to the same behavior before restriction), mainly in result-oriented acts (approaching the feeder, checking, etc.). Thus, in terms of restriction the behavioral cycle in one side of the cage changes the activity of neurons during the performance of acts that have preserved their effectiveness in behavior, and, accordingly, restructuring the structure of individual experience. To some extent, this effect is similar to the process of accommodative reconsolidation of the elements of previously formed experience during the formation of a new element of experience in learning processes (Alexandrov et al., 2018).

Despite the changes in the structure of individual experience when performance is restricted, this element of experience still remains. The sessions with the return of the previously removed pedal when the animals resumed their food-seeking behavior clearly demonstrate this. The studies in the restoration of instrumental food-seeking behavior after its 'extinction' (Trask et al., 2017) demonstrate that there is no 'erasure' of the extinguished experience. It is shown that when conducting a test session in the context opposite to the 'extinction' session, the behavior is restored. This resumption of behavior is considered as 'renewal' (Bouton & Bolles, 1979). In the AAB renewal studies the formation of the 'fear reaction' takes place in the context of A; 'extinction' – in the context of B; the test session – in the context of A (Bouton & Bolles, 1979; Bouton & King, 1983; Bouton & Peck, 1989). In the ABC renewal studies, the final testing takes place in the new context of C (Bouton & King, 1983; Bouton & Ricker, 1994). Besides, some studies describe the AAB renewal, formation, and 'extinction' in the context of A; the test session – in the new context of B (Thomas, Larsen, & Ayres, 2003; Laborda, Witnauer, & Miller, 2011; Tamai & Nakajima, 2000). All three options of extinction – renewal experiments were also carried out for instrumental behavior (Bouton, Todd, Vurbic, & Winterbauer, 2011; Todd, 2013).

These experiments showed that the 'extinction' of instrumental behavior does not 'erase' the initial learning.

Considering the importance of the data obtained for understanding the processes of adaptation to prohibition in humans, we should note that the results of recent studies of the possibilities and mechanisms of influence on the formed memory in animals (without the use of pharmacological agents) play an important role in developing innovative approaches to 'editing' and depressing human memory, especially traumatic memory and memory related to post-traumatic stress disorders) (Phelps & Hofmann, 2019).

***Conclusions**:*

Changes in the frequency of neuronal activity in terms of restriction are mainly associated with the loss of the ability to perform a result-oriented behavioral act. This speaks in favor the changes in the structure of individual experience, directly related to the impossibility of 'external' performance of one of its elements.

Changes in the activity of neurons in preserved behavior bring evidence for modifications affected not only the element of experience directly subjected to restriction but also the element associated with it, which do not contradicts to the concept of adaptive reconsolidation of experience.

In most cases the increase in the frequency of activity of neurons, changes in their activity, as well as certain behavioral parameters (i.e. the highest frequency of grooming in place of the removed pedal, an increase in the number of standings in terms of restriction) indicates a prolonged discoordination. Discoordination leads to changes in the structure of individual experience associated with both morphological and functional modifications of neurons and perhaps with the death of some neurons.

The experiments aimed at identifying the mechanisms influencing the formed memory in animals play an important role not only for basic research on the dynamics of human memory, but also for developing approaches to 'editing' memory.

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