Advances in Intelligent Systems and Computing 1358

Boris M. Velichkovsky
Pavel M. Balaban
Vadim L. Ushakov *Editors*

Advances in Cognitive Research, Artificial Intelligence and Neuroinformatics

Proceedings of the 9th International Conference on Cognitive Sciences, Intercognsci-2020, October 10–16, 2020, Moscow, Russia

Springer

Editors
Boris M. Velichkovsky
National Research Center
"Kurchatov Institute"
Moscow, Russia

Pavel M. Balaban
Institute of Higher Nervous Activity RAS
Moscow, Russia

Vadim L. Ushakov
Institute for Advanced Brain Studies
Lomonosov Moscow State University
Moscow, Russia

ISSN 2194-5357 ISSN 2194-5365 (electronic)
Advances in Intelligent Systems and Computing
ISBN 978-3-030-71636-3 ISBN 978-3-030-71637-0 (eBook)
https://doi.org/10.1007/978-3-030-71637-0

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Subserving of Task Switching in Rabbits' Cingulate Cortex Neurons

Alexey A. Sozinov[1,3(✉)], Yuri V. Grinchenko[1,2], Anastasia V. Bakhchina[1], Maria Zubtsova[3], and Yuri I. Alexandrov[1,2,3,4]

[1] Shvyrkov's Laboratory Neural Bases of Mind, Institute of Psychology, RAS, Moscow, Russia
sozinovaa@ipran.ru
[2] Moscow State University of Psychology and Education, Moscow, Russia
[3] State Academic University for the Humanities, Moscow, Russia
[4] Higher School of Economics, Moscow, Russia

Abstract. Interruption of one behavior and transition to the execution of another are associated with cognitive load that leads to a decrease in task performance. The details of incipience of stable performance after switching on the level of single neurons remain unclear. Here we address two issues concerning the involvement of neurons in subserving of behavioral execution. First, the behavioral difference between the first and subsequent trials after switching lacks full explanation in terms of engagement of neurons that underlies task performance. Second, we asked whether functionally similar neurons belong to the same or different putative types of cells. We propose that the task switching requires selection of neurons akin to reinstatement of learning. Therefore, we hypothesized that the after-switch dynamics of neuronal activity is related to the degree of the neuron's involvement in task execution. This link has been revealed in rabbits' anterior and posterior cingulate single-cell activity recorded during alternation of two instrumental appetitive behaviors. We imply that the view of switching as a learning episode seems to disentangle the relationship between several aspects of cingulate activity: conflict monitoring, initiation and control of behavior after switching, novelty, and memory retrieval – they all include reorganization of individual experience. No relationship was found between the specialization of neurons and their putative cell-type. Since the cell-type coincides with the metabolic properties of neurons, we assume that the functional assembly of neurons is derived from complementarity of their divergent properties.

Keywords: Task switching · Learning · Single neuron · Rabbit · Neuronal selection · Reorganization of memory · Functional system · Complementarity

1 Introduction

The interruption of one behavior and the transition to the execution of another are associated with a decrease in the effectiveness of alternating tasks performance. It is conventionally considered as a manifestation of "task-set" reconfiguration that requires cognitive effort [1]. The brain underpinnings of task-switching are often described in

B. M. Velichkovsky et al. (Eds.): Intercognsci 2020, AISC 1358, pp. 439–451, 2021.
https://doi.org/10.1007/978-3-030-71637-0_50

terms of involvement of brain areas, especially in functional-anatomy studies. Conventionally, anterior cingulate cortex (ACC) is necessary during onset of task execution after switching [2, 3], but see [4], whereas posterior cingulate (PCC) supports its subsequent maintenance [5]. Meanwhile, PCC has been recently described as having an important role in "cognitive control" [6, 7]. Depending on the novelty and predictability of switching, maintenance-related activity in ACC [8, 9], as well as involvement of PCC in alteration [6, 10] has been revealed in imaging, inactivation, and single-cell studies (see also [11]).

It is often not possible to identify a single area of the brain, necessary for changes in behavior, because switch-related activity is task-specific [12, 13]. Accordingly, single-neuron recordings in ACC show that the firing increases when the behavior needs to be changed [14], and that the task selectivity of firing decreases following a task switch [15]. In PCC neurons the firing increased from the switch to repeat trials [16]. At the same time ACC and PCC neurons show stable selectivity to different aspects of task performance during its maintenance [17–20]. The inconsistency of these results is further complicated by the fact that the difference of firing frequency between switch and repeat trials may not appear unless the neurons are grouped by their specialization, i.e. involvement in task execution [16].

The task-specific aspects of ACC and PCC activity [21–23], as well as dynamics of this activity along with training or time [24–28] have been revealed with various methods, including single-unit activity recording in rabbits [17, 29–33]. Namely, ACC and PCC have been proposed to provide memory retrieval at the early [28, 34] and late [24, 25, 35] stages of learning (see also [21, 36, 37]). The ambiguity of functional descriptions of the ACC and PCC (switching and maintenance; recent and remote memories) can be solved by the assumption that both "memory retrieval" and "cognitive effort" during switching require memory reorganization and selection of units for subserving of behavior. Presumably, this reorganization is the "reorganizational reconsolidation" [38], i.e. modification of structure of individual experience without formation of a new element within that structure. This modification has been described within the approach to behavior as manifestation of the systems structure of individual experience [39–41]. On the basis of this assumption we hypothesized, firstly, that the after-switch dynamics of neuronal activity is related to the degree to which a neuron is task-related (i.e. to which it is "involved" in task execution).

Experiments with neuronal activity recording where animals consumed alcohol showed that a group of neurons of one specialization can be heterogeneous: only part of them changed their task-related activity during alcohol intake [42]. Here we aimed at characterization of the systems organization of behavior by assessing the correspondence between the specialization of neurons and their putative cell type. Importantly, the data on the correspondence between functional properties of a neuron and its putative cell type can be based on electrophysiological measures [43], whereas cell-types define the metabolic properties of neurons [44]. When the function is considered as a computation or information coding, then the functional and physiological properties would be expected to correspond (e.g. [43, 45]). However, the activity of a neuron provides metabolic changes, rather than transfer of information [46]. From the functional systems view [47], the function is achievement of a result by a system of divergent elements in

brain and body, that conform their different degrees of freedom within a system and exchange their metabolic substrates. Developing this view, we propose, secondly, that the functional neuronal assemblies are constituted by various cell types – the latter are complementary in the sense of mutual cooperation in achieving the adaptive result (see also [48, 49]).

To address these issues, we recorded single-neuron activity in rabbits' ACC and PCC during switching between blocks of trials – cycles of two ways of food-acquisition, used by us previously (e.g., [17, 40, 50]). The rabbits have been successfully used in working memory setups (e.g., [51]). Therefore, we expected that the assessment of changes after transition from one behavior to another at the level of single neurons would unravel the incipience of stable performance after switching by covering both "cognitive effort" and "memory" descriptions of cingulate activity under the idea of reorganization of experience.

2 Methods

2.1 Subjects

Eight rabbits *Oryctolagus cuniculus* were food-deprived with ad libitum water to be trained in the experimental chamber (Fig. 1) to receive food. Their loss of weight did not exceed 15% from the weight of non-deprived animals of the same age. The experimental protocols are in accordance with the Council of the European Communities Directive of November 24, 1986 (86/609 EEC) and were approved by the ethics committee of the Institute of Psychology, Russian Academy of Sciences.

2.2 Behavioral Tasks and Training

The rabbits were trained to perform cyclic operant food-acquisition behavior on two symmetrical sides of the experimental chamber (Fig. 1, left), where each side is equipped with a pedal and a feeder in adjacent corners. A food pellet is delivered to the feeder if the corresponding pedal is pressed with paw(s) and if turning to the feeder is performed along the wall (the food is withdrawn if the animal turns to the center of the chamber on the way to the feeder).

The training started from the left side of the chamber for half of the animals to control for the differences between the two sides. The training was performed through 8 steps (Fig. 1, middle) made consecutively on each side of the experimental chamber: delivery of food to the feeder (steps 1 and 2), turning head and body from the feeder (3 and 4), turning to the pedal (5 and 6), pressing the pedal and turning to the feeder (7 and 8). These steps were also used to divide between acts within cycles of the resulting behavior with corresponding behavioral markers (Fig. 1, left) recorded in all sessions.

Each step of training is considered done if the criterion of 15 effective cycles in a row has been reached at any moment within a 40–60-min training session. After learning to press the pedal on two sides of the chamber separately (one side per session), the switching sessions are introduced, where the left and right sides of a symmetric chamber are made effective alternatively. The correct cycle was a loop (Fig. 1, right)

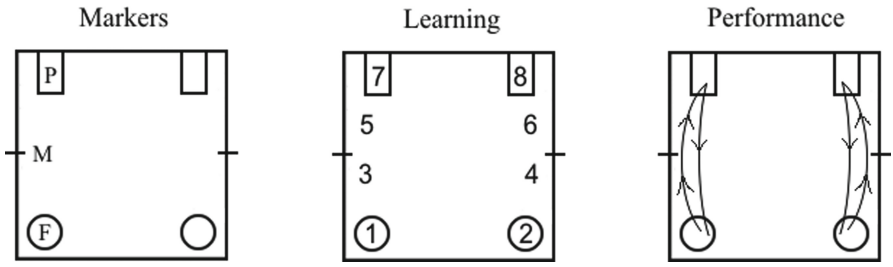

Fig. 1. The behavioral markers, order of learning, and cycles of alternated behaviors. Left. Schematic image of the experimental chamber with feeders (F) and pedals (P) on two symmetric sides. The actographic markers received from the chamber at all sessions including neuronal recordings are lowering the head into and raising the head from the feeders, crossing the middle line of the lateral walls (M), and pressing and releasing of the pedals. Middle. The order of steps of learning (1–8) in the same experimental chamber. Right. The resulting cycles of food-acquisition on the alternated sides of the chamber. See text for details.

from pressing a pedal through turning to corresponding feeder facing a wall to eating in the feeder, and turning back to the same pedal (if the effective side had not changed). A switch between the sides was initiated upon not less (and in most cases not more) than 7 effective cycles. These cycles (along with ineffective ones) constitute a block of cycles. The absence of food in the feeder after pressing the pedal along with delivery of food on the other side were the signals for switching.

2.3 Brain Activity Recording

The surgery procedures before training to press the pedals were followed by rest in a homecage with analgetics and no deprivation (not less than 3 days).The electrode intrusion started at the onset of switching sessions. Single-neuron activity was recorded with glass electrodes (2,5M KCl; 3–6 MOhm @ 1 kHz) from rabbits' anterior (AP-4 mm; ML ± 1−2mm; VD + 2–6 mm) or posterior (AP + 9 mm ; ML ± 1–2 mm) cingulate cortical areas during food-acquisition performed by alternating the blocks of cycles on each side of the experimental chamber. The signal from the electrode was pre-amplified with an in-lab-made head-stage, amplified with NBL-302 (Neurobiolab, Moscow, Russia), and digitized with E-14-140 external ADC (L-Card, Moscow, Russia), threshold-discriminated and sorted to identify spikes of single neurons with D-Main-4 in-lab software (Y. Raigorodski, A. Krylov).

Every record included at least one block of cycles on each side. The records were made in one cingulate area at a time for 3–5 days a week each. After two weeks the animals were sacrificed, their brains sliced and taken for morphological analysis to verify electrode location.

2.4 Variables and Data Analysis

The durations of movements from raising the head from the feeder to pressing the pedal (duration of approaching the pedal) and from pressing the pedal to lowering the head into

the feeder (duration of returning to the feeder) were estimated on the basis of behavioral markers (Fig. 1, left). The number of ineffective acts from each shifting of the effective side by the experimenter (i.e. from the end of the last effective cycle) on one side to the start of the first effective cycle on the other side was count to assess the pace of switching.

The frequency of spikes was calculated for each behavioral act of each neuron, as well as the mean frequency for the whole session. All recorded cells were categorized as either "specialized" (in relation to a system of a behavioral act) or "unidentified" on the basis of probability of its activations in the separate acts (see Fig. 2). The significant increase of the firing rate above average frequency for the whole record that exceeds the factor of 1.5 in a given act was termed activation. If this probability reaches 100% in one or more acts, then the neuron is considered specialized, and the activations of a given act are called "specific" activations (see [40, 52] for more details). An illustration of a specific activation of a specialized neuron is presented in Fig. 3.

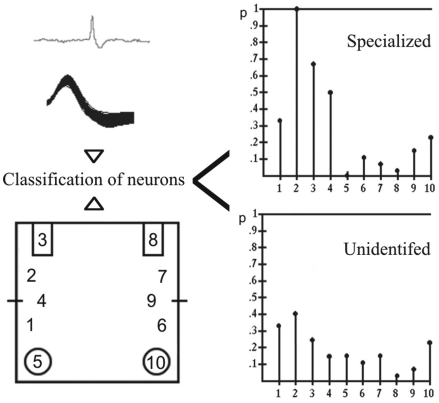

Fig. 2. Recording and analysis of neuronal activity includes digitizing raw signal, off-line sorting spikes after threshold discrimination (top left), and classification of neurons with respect to the acts of behavior (1–10): turning from the feeder, turing to the pedal, pressing the pedal and turning from the pedal to the middle of the lateral wall, and acquiring the food pellet from the feeder in the left (1–5) and right (6–10) sides of the experimental chamber (bottom left). The specialized neurons have at least one act with 1.0 activation probability (act #2 in a PCC neuron, top right), whereas unidentified neuron does not (a neuron with activation probability less than 1.0 in all acts, bottom right).

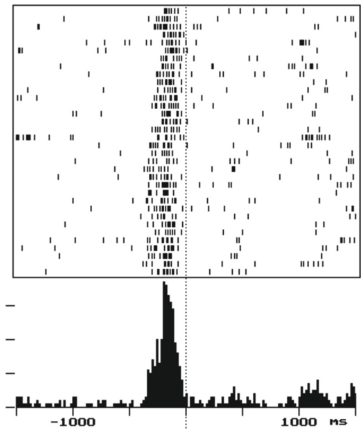

Fig. 3. The raster plot of a specialized PCC neuron with spikes (dashes) during successive turns of the animal towards a feeder vertically aligned to crossing the middle of the wall of the chamber. Below is the histogram of these spikes (20 ms in a bin, the ticks of the ordinate show tens of spikes) on the timeline with 500 ms division.

We defined putative cell types of all recorded neurons by clustering (hierarchical and K-means) using two measures of spike width (duration from initial negativity

inflection point to trough and trough-to-peak duration), average firing rate, and depth in the cortex [43]. The spike-width parameters were extracted from the raw recordings before filtering. The correspondence between the specializations and clusters of neurons was assessed by Pearson's chi-square criterion. Pairwise comparisons of the electrophysiological measures between specializations (corrected) were performed with Mann-Whitney test.

To assess the changes after switching, in each block of cycles the measures of behavior and neuronal firing were assessed for the first, the second, and a median of not less than four subsequent cycles. These cycles were labeled "C1", "C2", and "C3", correspondingly. Consequently, a block was subjected to the analysis if the data had been recorded during not less than 6 effective cycles of behavior on each side of the experimental chamber after switching within the given record.

Two types of neuronal firing analyses were employed to assess the changes of brain activity after switch. First, the blocks with intermittent errors along with blocks of at least 6 effective cycles in a row were taken to assess the firing frequency. We decreased the sample of these records by removing unidentified cells with probability of activation that exceeds 0.6 (i.e. those with activations earlier called "non-specific", see [40]). An act with maximal average frequency was identified for expressing all frequencies in the units of this maximal average. A neuron was not included in this analysis if the side of the act with maximal frequency was not the side of the analyzed block.

Second, the removal of the blocks where ineffective feeder checking interrupted consecutive effective cycles has led to a dramatic decrease of available cases, since it is common for the rabbits to check the empty feeder even at the asymptotic performance level. Raw spike frequencies were used for this analysis, because the average frequencies in acts with low activation probability (less than 0.6) were estimated for each neuron (both specialized and unidentified) and compared separately from average frequencies in specific acts of specialized neurons. The recording of activity of a neuron could contain more than one switching with subsequent 6 or more effective cycles in a row, giving more that one case for one neuron in this analysis.

Calculation of firing frequency and movement durations were made with in-lab software D-Main-4 and Neuru (A. Krylov). The statistical analysis and graphics were performed with SPSS 11.0 and Python coding in IDLE.

3 Results

3.1 Behavioral Measures

The duration of behavioral cycles, as well as durations of pedal approaching and returning to the feeder did not differ between the groups with the left and right side of experimental chamber as the starting side (Mann-Whitney $U > 1000$; $p > 0{,}6$). The duration of behavioral cycles increased after switching. This difference was significant for comparisons between C1 and C3 (Wilcoxon test, $Z = -2.01$; $p = 0.044$), as well as C2 and C3 ($Z = -2.06$; $p = 0.040$) and was due to the successive increase of duration of returning to the feeder (C1-C3: $Z = -2.50$; $p = 0.012$. C2-C3: $Z = -1.87$; $p = 0.062$. Friedman test,

$p < 0.005$), whereas the duration of approaching the pedal did not change ($p > 0.4$ for all comparisons).

An additional analysis revealed that the duration of the whole cycle also differs between two consecutive weeks of the experiment: the duration of the cycles is higher during the second period in comparison to the first ($U = 829.0$; $p < 0.01$). The number of ineffective acts during the transition during the second period was less than that during the first period for the side of the experimental chamber trained first. The nonparametric Mann-Whitney criterion showed this difference at the trend level ($U = 1151.5$; $p = 0.065$), whereas it reached significance with the parametric T-criterion ($t_{110} = 2.09$; $p = 0.039$). Similar difference for the side trained second had the opposite direction, but was not significant ($U = 1194.0$; $t107 = -1.51$; $p > 0.1$). Repeated measures ANOVA revealed the interaction of the Period and Side ($F_{1,62} = 4.14$; $p = 0.046$).

3.2 Neuronal Activity

One hundred and fourty three single cells were selected for the analysis of firing dynamics after switching out of 214 that were recorded on the basis of their anatomic localization and the quality of spike sorting.

Blocks of Cycles with Errors. The analysis of data that included blocks of cycles with errors included 86 neurons with maximal frequency on the same side as the switching. Exclusion of task-related units left 63 neurons in the contrasting groups of specialized cells and cells with probability of activation that does not exceed 0.6. The specialized and unidentified neurons were characterized by opposite changes of the spikes frequency after switching (Fig. 4A). Namely, in the ACC, the spike frequency of specialized neurons increased, and that of the unidentified neurons decreased after switching, the difference achieving significance between the specialized and unidentified units in C3 ($U = 45.0$; $p = 0.006$). Separate ANOVA for the C3 has revealed the interaction of Specialization and Brain Area ($F_{1,59} = 5.59$; $p = 0.021$). In the PCC, the frequency of spikes decreased in specialized neurons. The similar analysis for C1 did not reveal significant differences ($p > 0.2$). However, if any, the changes in the PCC were in the opposite direction[1].

Blocks of Cycles without Errors. The analysis of data that excluded blocks of cycles with errors was performed for each switching. Consequently, 77 switches with corresponding spike frequencies were analyzed. The number of specialized neurons in this sample of neurons recorded with cycles without errors did not allow for separate analysis of ACC and PCC neurons. The combined sample has shown the dynamics similar to that of ACC in blocks of cycles with errors (Fig. 4B). Thus, the frequency in the specific acts increased after switching from C1 to C2 (Wilcoxon test, $Z = -2.10$; $p = 0.036$, the difference between C1 and C3 was at the tendency level $Z = -1.82$; $p = 0.069$), whereas the frequency in the acts with low activation probability decreased from C2 to C3 ($Z = -2.64$; $p = 0.008$, the difference between C1 and C3 was at the tendency level $Z = -2.70$; $p = 0.095$).

[1] Although the changes of firing frequency of PCC neurons were less consistent, repeated measures ANOVA has revealed interaction of Cycle, Brain Area, and Specialization ($F_{2,118} = 3.38$, $p = 0.041$). However, the corresponding distributions differed from normal, and the lower-bound significance without sphericity assumption had been 0.71.

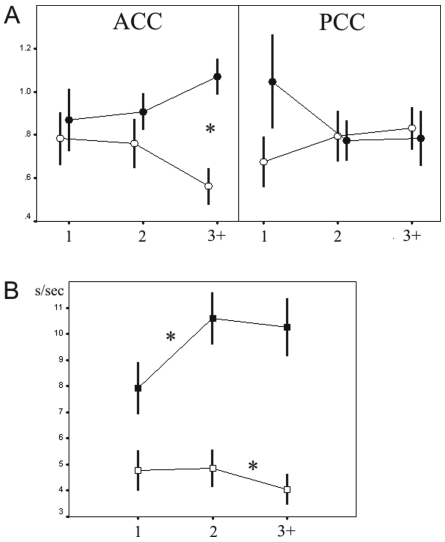

Fig. 4. The firing of specialized cells in specific acts after switching differed from firing in other acts and firing of unidentified cells. A. Spike frequency of specialized (black dots) and unidentified (white dots) cells in the units of maximal average frequency in ACC and PCC in the first, second, and median of at least four subsequent effective cycles in a row after switching (average ± SEM). The asterisk signifies significant differences ($p < 0{,}05$). B. Spike frequency of all cells in specific acts (black squares) and acts with low activation probability (white squares). Marked as in Fig. 4.

Putative Cell-Types. The analysis of putative cell-type relation to the specialization of neurons involved a sample of 113 neurons that had no missing values of the electrophysiological measures. Three clusters of cells have been identified on the basis of linkage distance with the most significant contribution of trough-to-peak duration (one-way ANOVA, $F_{110} = 321.09$; $p < 0.00001$). Two of the clusters with average trough-to-peak durations of 0.523 and 0.962 ms could be considered as putative inhibitory interneurons and putative pyramidal neurons, correspondingly (see Kawai et al. 2018). No correspondence between the specializations and clusters have been revealed (Pearson's χ^2; $p > 0{,}35$). Moreover, each of the clusters contained all of the specializations as well as unidentified neurons. Pairwise comparisons of the electrophysiological measures between clusters and specializations (corrected) have also not revealed significant differences (Mann-Whitney U, $p > 0{,}1$). If any, feeder-approaching neurons were found in deeper layers of posterior cingulate cortex, than the neurons specialized in relation to a preceding act of leaving the pedal (Kruskal-Wallis $H = 10{,}21$; $p = 0{,}016$), but the corresponding pair-wise differences were not significant.

4 Discussion

We checked whether the after-switch dynamics of neuronal subserving of behavior is related to the degree of the neuron's involvement in task execution, and whether the

specialization of neurons corresponds to their putative cell type. This was done by recording the single-neuron activity in rabbits' ACC and PCC during alternation of two ways of operant appetitive behaviors. At this sample of neurons no relationship was found between the specialization of neurons and their putative cell-type: each cluster contained cells of all the specializations. This result is consistent with the assumption of heterogeneity of a group of neurons specialized in relation to a system of the same act of behavior. The putative cell-types are presumably related to metabolic properties of neurons (see [44]) besides their electrophysiological and morphological properties [53]. The contacts between neurons can be based on metabolic cooperation [54] and serve the metabolic needs of the cells [47]. Therefore, we consider the functional assembly of neurons to be derived from complementarity of their divergent properties.

The changes of firing of the neurons after switch did show functional relevance that differed between the two brain areas. Thus, the firing of specialized cells, i.e. cells necessary for the corresponding functional system, increased after switching, whereas the activity in other acts and firing of unidentified cells decreased. The effect was clearly evident in ACC, whereas PCC neurons did not show significant changes. This result is in correspondence with the previously described increase in the selectivity of neuronal firing in ACC after switching [15]. However, to our knowledge, this is the first demonstration of selectivity increase in cells of different involvement in subserving of behavior.

The dynamics of firing shown here for the ACC and PCC shows that greater activation of ACC in switch trials in relation to repeat trials revealed in functional anatomy studies, as well as the opposite PCC activation [5, 28] (but see [4]), might emerge from the activity of quantitatively prevailing units that do not specifically underpin task execution. In other words, the dynamics of "activations" in functional-anatomy studies does not reveal specific task-execution activity. Rather, it is due to activity of neurons without specific involvement. As argued earlier [42], unidentified neurons are specialized in relation to systems behavioral acts other than those formed in our setup. Therefore, the differences revealed presumably manifest the processes of reorganization of experience. Accordingly, task switching shares characteristics of novelty [55], and the onset of previously learned behavior after switching can be a selective process akin to reinstatement of learning (see [41]).

The change of speed after switching has not revealed any effects similar to "switch cost" [56], common for switching studies [1, 9]. Moreover, the duration of returning to the feeder in effective cycles increases after switching (as well as during repetitive overtraining during the experiment). Since the duration of approaching the pedals does not differ between successive cycles after switching, this effect can be explained by changes of motivation.

The rate of switching appeared to be associated with the history of learning the alternated behaviors: at the beginning of alternation, the transition to the first side was faster than to the second. These contrasts disappeared along with further training.

Variability and dynamics of switching are commonly explained by cognitive control process [1, 3, 4, 6]. We consider switching as a behavior that resembles learning and involves modification of prior experience [38, 49]. Behavior and brain activity analyses show that task alternation requires learning, principally similar to acquisition of the tasks

proper [57]. Accordingly, switch-related brain activity is task-specific, rather than characteristic of a certain brain area[2]. Additionally, if the task switching requires formation of a new experience, we would expect the switch accuracy increase to be accompanied by the dynamics of interplay between the novel switching experience and the earlier formed task experience. This is to be verified in further studies, but the relation of switching rate to the order of learning may manifest this interplay.

5 Conclusion

Although task switching is alternation of behaviors that are known to the individual, every transition includes novelty and can be considered as a behavioral adaptation, or reorganization of experience. Therefore, starting a previously learned behavior can be viewed as reorganization of brain activity akin to learning, revealed here as increase of task-specific neuronal activity after switching in two areas of cingulate cortex. The functional groups of neurons that underpin newly formed behavior are proposed to consist of diverse cells that unite of the basis of complementarity of their properties.

Acknowledgements. The study had been supported by Russian Foundation for Basic Research, grant #17-06-00653. The analysis of spike width and other correlates of cell type is performed in the framework of the State assignment of Ministry of Science and Higher Education of Russia (No. 0159-2019-0001 for the Institute of Psychology RAS).

Conflict of Interest. The authors declare no conflict of interest.

References

1. Monsell, S.: Task switching. Trends Cogn. Sci. **7**, 134–140 (2003). https://doi.org/10.1016/S1364-6613(03)00028-7
2. Hyafil, A., Summerfield, C., Koechlin, E.: Two mechanisms for task switching in the prefrontal cortex. J. Neurosci. **29**, 5135–5142 (2009). https://doi.org/10.1523/JNEUROSCI.2828-08.2009
3. Machinskaya, R.I.: The brain executive systems. Zh. Vyssh. Nerv. Deiat. Im. I P Pavlova. **65**, 33–60 (2015). https://doi.org/10.7868/s0044467715010086
4. Premereur, E., Janssen, P., Vanduffel, W.: Functional MRI in macaque monkeys during task switching. J. Neurosci. **38**, 10619–10630 (2018). https://doi.org/10.1523/JNEUROSCI.1539-18.2018
5. Sohn, M.H., Ursu, S., Anderson, J.R., Stenger, V.A., Carter, C.S.: The role of prefrontal cortex and posterior parietal cortex in task switching. Proc. Natl. Acad. Sci. U. S. A. **97**, 13448–13453 (2000). https://doi.org/10.1073/pnas.240460497
6. Pearson, J.M., Heilbronner, S.R., Barack, D.L., Hayden, B.Y., Platt, M.L.: Posterior cingulate cortex: Adapting behavior to a changing world. Trends Cogn. Sci. **15**(4), 143–51 (2011). https://doi.org/10.1016/j.tics.2011.02.002

[2] According to our approach, the view of function as a product of a brain area is considered entrapping (see refs 37, 39, 41, and 47).

7. Nelson, A.J.D., Hindley, E.L., Haddon, J.E., Vann, S.D., Aggleton, J.P.: A novel role for the rat retrosplenial cortex in cognitive control. Learn. Mem. **21**, 90–97 (2014). https://doi.org/10.1101/lm.032136.113
8. Ma, L., Chan, J.L., Johnston, K., Lomber, S.G., Everling, S.: Macaque anterior cingulate cortex deactivation impairs performance and alters lateral prefrontal oscillatory activities in a rule-switching task. PLoS Biol. **17**, e3000045 (2019)
9. Umemoto, A., Holroyd, C.B.: Exploring individual differences in task switching: Persistence and other personality traits related to anterior cingulate cortex function. Prog. Brain Res. **229,** 189–212 (2016). https://doi.org/10.1016/bs.pbr.2016.06.003
10. Poulsen, C., Luu, P., Davey, C., Tucker, D.M.: Dynamics of task sets: evidence from dense-array event-related potentials. Cogn. Brain Res. **24**, 133–154 (2005). https://doi.org/10.1016/j.cogbrainres.2005.01.008
11. Ng, C.W., Noblejas, M.I., Rodefer, J.S., Smith, C.B., Poremba, A.: Double dissociation of attentional resources: prefrontal versus cingulate cortices. J. Neurosci. **27**, 12123–12131 (2007). https://doi.org/10.1523/JNEUROSCI.2745-07.2007
12. Calcott, R.D., Berkman, E.T.: Neural correlates of attentional flexibility during approach and avoidance motivation. PLoS ONE **10**, e0127203 (2015)
13. Dreher, J.C., Koechlin, E., Ali, S.O., Grafman, J.: The roles of timing and task order during task switching. Neuroimage **17**, 95–109 (2002)
14. Bryden, D.W., Brockett, A.T., Blume, E., Heatley, K., Zhao, A., Roesch, M.R.: Single neurons in anterior cingulate cortex signal the need to change action during performance of a stop-change task that induces response competition. Cereb. Cortex. **29**, 1020–1031 (2019). https://doi.org/10.1093/cercor/bhy008
15. Johnston, K., Levin, H.M., Koval, M.J., Everling, S.: Top-down control-signal dynamics in anterior cingulate and prefrontal cortex neurons following task switching. Neuron **53**, 453–462 (2007). https://doi.org/10.1016/j.neuron.2006.12.023
16. Alexandrov, Y.I., Shevchenko, D.G., Gorkin, A.G., Grinchenko, Y.: V: Dinamics of systems organization of behavior during consecutive trials [Dinamika sistemnoj organizacii povedenija v ego posledovatel'nyh realizacijah]. Psikholog. Zh. **20**, 82–89 (1999)
17. Alexandrov, Y.I., Grinchenko, Y.V., Järvilehto, T.: Change in the pattern of behavioural specialization of neurons in the motor cortex of the rabbit following lesion of the visual cortex. Acta Physiol. Scand. **139**, 371–385 (1990)
18. Gorkin, A.G., Shevchenko, D.G.: Stability of the behavioral specialization of neurons. Neurosci. Behav. Physiol. **21**, 222–229 (1991)
19. Sozinov, A.A., Averkin, R.G., Grinchenko, Y.V., Alexandrov, Y.I.: Involvement of previous memory in learning and the transfer effect. Int. J. Psychophysiol. **69**, 258 (2008). https://doi.org/10.1016/j.ijpsycho.2008.05.179
20. Weible, A.P., Rowland, D.C., Pang, R., Kentros, C.: Neural correlates of novel object and novel location recognition behavior in the mouse anterior cingulate cortex. J. Neurophysiol. **102**, 2055–2068 (2009)
21. Gabriel, M.: Discriminative Avoidance Learning: A Model System. In: Neurobiology of Cingulate Cortex and Limbic Thalamus. pp. 478–523. Birkhäuser Boston (1993)
22. Kuzina, E.A., Alexandrov, Y.I.: Differences in neuronal subserving of instrumental behavior, formed by one- and multi-stage learning procedures. Zhurnal Vyss. Nervn. Deyatelnosti im. I.P. Pavlov. **69**, 601–617 (2019)
23. Tse, D., Takeuchi, T., Kakeyama, M., Kajii, Y., Okuno, H., Tohyama, C., Bito, H., Morris, R.G.M.: Schema-dependent gene activation and memory encoding in neocortex. Science **333**, 891–895 (2011). https://doi.org/10.1126/science.1205274
24. Corcoran, K.A., Yamawaki, N., Leaderbrand, K., Radulovic, J.: Role of retrosplenial cortex in processing stress-related context memories. Behav. Neurosci. **132**, 388–395 (2018). https://doi.org/10.1037/bne0000223

25. Frankland, P.W., Ding, H.K., Takahashi, E., Suzuki, A., Kida, S., Silva, A.J.: Stability of recent and remote contextual fear memory. Learn. Mem. **13**, 451–457 (2006). https://doi.org/10.1101/lm.183406
26. Insel, N., Takehara-Nishiuchi, K.: The cortical structure of consolidated memory: a hypothesis on the role of the cingulate-entorhinal cortical connection. Neurobiol. Learn. Mem. **106**, 343–350 (2013). https://doi.org/10.1016/j.nlm.2013.07.019
27. Kuzina, E.A., Gorkin, A.G., Aleksandrov, Y.I.: Neuron activity in the retrosplenial cortex of the rat at the early and late stages of memory consolidation. Neurosci. Behav. Physiol. **46**, 789–793 (2016)
28. Tracy, J., Flanders, A., Madi, S., Laskas, J., Stoddard, E., Pyrros, A., Natale, P., DelVecchio, N.: Regional brain activation associated with different performance patterns during learning of a complex motor skill. Cereb. Cortex. **13**, 904–910 (2003)
29. Alexandrov, Y.I., Grinchenko, Y.V., Shevchenko, D.G., Averkin, R.G., Matz, V.N., Laukka, S., Korpusova, A.V.: A subset of cingulate cortical neurones is specifically activated during alcohol-acquisition behaviour. Acta Physiol. Scand. **171**, 87–97 (2001). https://doi.org/10.1046/j.1365-201X.2001.00787.x
30. Freeman, J.H., Gabriel, M.: Changes of cingulothalamic topographic excitation patterns and avoidance response incubation over time following initial discriminative conditioning in rabbits. Neurobiol. Learn. Mem. **72**, 259–272 (1999)
31. Gorkin, A.G., Shevchenko, D.G.: Distinctions in the neuronal activity of the rabbit limbic cortex under different training strategies. Neurosci. Behav. Physiol. **26**, 103–112 (1996). https://doi.org/10.1007/BF02359413
32. Sozinov, A.A., Laukka, S.J., Tuominen, T., Siipo, A., Nopanen, M., Alexandrov, Y.I.: Transfer of simple task learning is different in approach and withdrawal contexts. Procedia Soc. Behav. Sci. **69**, 449–457 (2012)
33. Talk, A., Kashef, A., Gabriel, M.: Effects of conditioning during amygdalar inactivation on training-induced neuronal plasticity in the medial geniculate nucleus and cingulate cortex in rabbits (Oryctolagus cuniculus). Behav. Neurosci. **118**, 944–955 (2004). https://doi.org/10.1037/0735-7044.118.5.944
34. Bontempi, B., Laurent-Demir, C., Destrade, C., Jaffard, R.: Time-dependent reorganization of brain circuitry underlying long-term memory storage. Nature **400**, 671–675 (1999). https://doi.org/10.1038/23270
35. Frankland, P.W., Bontempi, B., Talton, L.E., Kaczmarek, L., Silva, A.J.: The involvement of the anterior cingulate cortex in remote contextual fear memory. Science **304**, 881–883 (2004). https://doi.org/10.1126/science.1094804
36. Smith, D.M., Miller, A.M.P., Vedder, L.C.: The retrosplenial cortical role in encoding behaviorally significant cues. Behav. Neurosci. **132**, 356–365 (2018)
37. Weible, A.P.: Remembering to attend: The anterior cingulate cortex and remote memory. Behav. Brain Res. **245**, 63–75 (2013)
38. Aleksandrov, Y.I.: Learning and memory: Traditional and systems approaches. Neurosci. Behav. Physiol. **36**, 969–985 (2006)
39. Alexandrov, Y.I.: How we fragment the world: the view from inside versus the view from outside. Soc. Sci. Inf. **47**, 419–457 (2008)
40. Alexandrov, Y.I., Sozinov, A.A., Svarnik, O.E., Gorkin, A.G., Kuzina, E.A., Gavrilov, V.V.: Neuronal bases of systemic organization of behavior. In: Advances in Neurobiology. pp. 1–33. Springer, New York LLC (2018)
41. Shvyrkov, V.B.: Behavioral specialization of neurons and the system-selection hypothesis of learning. In: Klix, F., Hagendorf, H. (eds.) Human memory and cognitive capabilities. pp. 599–611. North-Holland: Elsevier, Amsterdam (1986)

42. Alexandrov, Y.I., Grinchenko, Y.V., Laukka, S.J., Järvilehto, T., Matz, V.N., Korpusova, A.V.: Effect of ethanol on hippocampal neurons depends on their behavioural specialization. Acta Physiol. Scand. **149**, 105–115 (1993). https://doi.org/10.1111/j.1748-1716.1993.tb09598.x
43. Trainito, C., von Nicolai, C., Miller, E.K., Siegel, M.: Extracellular spike waveform dissociates four functionally distinct cell classes in primate cortex. Curr. Biol. **29**, 2973−2982.e5 (2019). https://doi.org/10.1016/j.cub.2019.07.051
44. Pinto, L., Dan, Y.: Cell-type-specific activity in prefrontal cortex during goal-directed behavior. Neuron **87**, 437–450 (2015)
45. Zaitsev, A.V., Lewis, D.A.: Functional properties and short-term dynamics of unidirectional and reciprocal synaptic connections between layer 2/3 pyramidal cells and fast-spiking interneurons in juvenile rat prefrontal cortex. Eur. J. Neurosci. 38, (2013). https://doi.org/10.1111/ejn.12294
46. Edelman, G., Finkel, L.: Neuronal group selection in the cerebral cortex. In: Dynamic aspects of neocortical function. pp. 653–695. New York (1984)
47. Anokhin, P.K.: Biology and Neurophysiology of the Conditioned Reflex and Its Role in Adaptive Behavior. Pergamon Press, New York (1974)
48. Alexandrov, Y.I., Alexandrova, N.L.: Subjective experience and culture. structure and dynamics. Soc. Sci. A Q. J. Russ. Acad. Sci. **38**, 109–124 (2007)
49. Alexandrov, Y.I., Gorkin, A.G., Sozinov, A.A., Svarnik, O.E., Kuzina, E.A., Gavrilov, V. V: Consolidation and reconsolidation of memory: a psychophisiological analysis. Vopr. Psikhol. **3**, 133–144 (2015)
50. Sozinov, A.A., Kazymaev, S.A., Grinchenko, Y.V., Alexandrov, Y.I.: Percent of task-specialized cingulate cortex neurons does not change during training. In: FENS Abstracts, p. 114.08 (2012)
51. Weible, A.P., McEchron, M.D., Disterhoft, J.F.: Cortical involvement in acquisition and extinction of trace eyeblink conditioning. Behav. Neurosci. **114**, 1058–1067 (2000). https://doi.org/10.1037/0735-7044.114.6.1058
52. Alexandrov, Y.I., Grinchenko, Y.V., Shevchenko, D.G., Averkin, R.G., Matz, V.N., Laukka, S., Sams, M.: The effect of ethanol on the neuronal subserving of behavior in the hippocampus. J. Behav. Brain Sci. **03**, 107–130 (2013)
53. Barthó, P., Hirase, H., Monconduit, L., Zugaro, M., Harris, K.D., Buzsáki, G.: Characterization of neocortical principal cells and interneurons by network interactions and extracellular features. J. Neurophysiol. **92**, 600–608 (2004)
54. Subak-Sharpe, H., Bürk, R.R., Pitts, J.D.: Metabolic Co-Operation Between Biochemically Marked Mammalian Cells in Tissue Culture. J. Cell Sci. 4, (1969)
55. Barcelo, F., Escera, C., Corral, M.J., Periáñez, J.A.: Task switching and novelty processing activate a common neural network for cognitive control. J. Cogn. Neurosci. **18**, 1734–1748 (2006). https://doi.org/10.1162/jocn.2006.18.10.1734
56. Rogers, R.D., Monsell, S.: Costs of a predictible switch between simple cognitive tasks. J. Exp. Psychol. Gen. **124**, 207–231 (1995)
57. Timofeeva, N.O., Kotlyar, B.I., Popovich, L.D.: Analysis of the neuronal mechanism of conditioned-reflex switching. Neurosci. Behav. Physiol. **14**, 146–152 (1984). https://doi.org/10.1007/BF01185222