



Brain Mechanisms of Embodied Decision-Making

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Abstract: One of the ways to comprehend mental abilities of individuals is to examine their underlying neural processes and mechanisms. To explore the role of cingulate cortical neurons in “mental rehearsal” immediately before every trial of appetitive instrumental task in well-trained animals, we analyzed recorded single-unit activity in relation to the task-relevant events during task trials and during delay periods inside each trial in the same animals. The results showed that neuronal activity in the rabbit posterior cingulate cortex during the delay consisted mostly of activity of those neurons which were specialized in relation to this task, though the delay periods were not intended to remember previous events. The data indicated that these neuronal groups are involved in the processes of unfolding planned future behavior. Sequences of neuronal events during the delay period (i.e. during “covert behavior” phase), used for decision making, depended on the role of neuron in overt behavior. During delay periods replays (or preplays) started with activity of very selective (“narrow selective”) neurons, specialized in relation to concrete behavioral acts, but late in the delay included activity of such “broadly selective” neurons which might have been related to movements similar in broad categories of behavior. Such results indicate that task-related neurons with different degree of selectivity are all involved in overt and covert phase of experience actualization, which might imply that decision making in rabbits is the embodied cognitive process.

Keywords: mental rehearsal, embodied cognition, posterior cingulate cortex, rabbit, decision making.

Introduction

How any organism selects an action among multiple alternatives is the biggest question in psychobiology and neuroscience. Decision making studies show that these processes, though in different applications, still share common elements including deliberation and commitment (Gold and Shadlen 2007), and in this sense this question is closely related to the phenomenon of mental rehearsal. According to Dennet (1996), reactivation of overt behavior in the inner environment has an evolutionary advantage.

Deliberation may include both action preparation and expected consequences of actions (e.g., Anokhin 1974; van der Meer and Redish 2010). One hypothesis is that action preparation is based on low pre-activation of the same neurons that are related to the movement itself (Murakami and Mainen 2015). In this case a neuron related to some movement appears to gradually increase its activity at subthreshold level during decision period and demonstrate a constant high level of activation just before the action (e.g. Gold and Shadlen 2007), but it is not might be always the case. At the same time, low-frequency activity was also noted during decision making periods. Replays as low-frequency neuronal activity occur during awake rest periods (e.g. Foster and Wilson 2006; Singer et al. 2013) and sleep (e.g. O'Neill et al. 2010). Such replays of activity during rest periods is evident also in immediate early gene transcription patterns (e.g. Arc), which reoccurs partly in those task-related neurons that were active during the deployment of overt behavior itself (Gheidi, Satvat and Marrone, 2012).

Task-related neurons in many cortical areas of the brain often exhibit the same activity patterns during delay periods before any actual motions as during the movement itself (e.g. Cisek and Kalaska 2004). Such activities might be a neuronal basis of covert mental rehearsal (Cisek and Kalaska 2004). This mental rehearsal might be related to the movements themselves or to more abstract information, which is not directly linked to movements per se (Freedman and Assad 2011). Motor imagery (the mental

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rehearsal of movement) may even result in learning without prior practice (Ingram et al., 2016). Most paradigms in which such neuronal activity is analyzed consists of delay periods between a sample and a target (e.g. Bisley et al., 2004), and in such cases neuronal activities often reflect properties of a sample memorized, namely working memory.

Neurons of many areas across many species show in delay periods activity related to goals, intended movements, trajectories: for example, frontal and parietal cortical neurons (Andersen and Cui, 2009; Park et al., 2014), motor cortical neurons (Churchland et al., 2010), premotor cortical neurons (Crammond and Kalaska, 2000), hippocampal neurons (Catanese et al., 2012). Several studies have reported that anterior cingulate cortex, also in humans, is playing a role in decision making (Rushworth et al., 2004; Walton, Devlin and Rushworth, 2004; Tervo et al., 2014). It was shown that posterior cingulate cortex is activated in humans during mental travels to the past and to the future (Viard et al., 2011), visuospatial imagery (Whittingstall et al., 2014) and during mental imagery of complex sequential limb movement (Sauvage et al., 2015). If such imagery is evident in the posterior cingulate cortex in animals other than humans is not known. It was stated recently that neurons of the posterior cingulate cortex (the retrosplenial cortex) play a key role in a range of cognitive functions, including episodic memory, navigation, imagination and planning for the future (Vann et al., 2009). Posterior cingulate cortex of rabbits has homologies to the ones in rodents and humans (Vogt, 2016). It was shown that task-related neurons have different types of specializations – more specific (related to concrete acts) or less specific (related to broad categories of behavioral acts and, in general, less differentiated experience) (e.g., Svarnik et al., 2005; Alexandrov et al., 2018).

The present study was aimed to figure out if mental rehearsal might be found in rabbits and if differently specialized neurons, including neurons specialized in relation to overt motor behavior, play different roles in such embodied mental rehearsal. We registered neuronal activity in rabbit posterior cingulate cortex during delay periods that did not require an animal to remember previous information and found that in these cases task-related neuronal replays were still evident, moreover replays consisted of neurons with different degree of task-selectivity.

Materials and Methods

Animals

Recordings were performed in 6 adult male rabbits (*Oryctolagus cuniculus*; weight about 3 kg). Food was continually available in the home cage except for the days of recordings. Their loss of weight did not exceed 15% from the weight of non-deprived animals of the same age. All surgical and experimental protocols were performed in accordance with National Institutes of Health guide for the care and use of Laboratory animals (NIH Publications No. 8023, revised 1978).

Behavioral paradigm

All rabbits were taught to obtain food following pedal-press in the experimental chamber with two pedals and two feeders (described in details in Alexandrov, Grinchenko and Jarvilehto, 1990). Pedal pressing activated an automatic feeder on the same side of the chamber, a pedal and a feeder were in adjacent corners. Each rabbit was to perform consecutive pedal-press task trials: pressing the pedal, turning to the feeder and taking food from the feeder at both sides of the cage. Each one side block consisted of 10-20 trials. No cue indicated the switch between the blocks. The two pedals were never active simultaneously. Infrared sensors placed inside the experimental cage monitored the position of the animal in the cage and the onset and offset of the behavioral acts.

Delay period

Following completion of pedal press shaping the delay period trials were introduced. Periodically both pedals were manually covered by a nontransparent shutter while an animal was in the middle of the experimental chamber facing the shutter. Then one of two pedals was taken out of the chamber. The flash (50 μ sec long, 0,3 Joule) indicated the beginning of the shutter opening; the full opening took less than 250 msec. Thus, the delay period lasted no longer than 250 msec. The decision-making process could be started before the shutter was fully opened.

Electrophysiological recordings

After the task acquisition, rabbits were implanted with microelectrodes. For all surgical procedures, which were performed under aseptic conditions, the animals were initially anesthetized with novocaine (8-

12 ml) injected subcutaneously. Craniotomies were made over posterior cingulate cortex and a custom-made recording chamber was fixed to the skull. The chamber was 3 mm in diameter and was attached to the skull by a ring of bone cement anchored by 3 screws evenly distributed around the craniotomy. Electrophysiological and behavioral recording techniques, as well as the criteria for the classification of the behavioral specialization of the units have been described in details elsewhere (e.g. Svarnik et al., 2005; Alexandrov et al., 2018).

Unit activity was recorded from the posterior part of Area 30 Complex (pA30C) and p29b-29e of the cingulate cortex ($P=11.1 \pm 0.3$; $L=3.3 \pm 0.1$, according to Vogt, 2016). Glass microelectrodes with 2.5 m KCl, tips of 1-3 μm diameter and impedance of 1-5 $\text{M}\Omega$ at 1.5 kHz were used and driven by a custom-made micromanipulator. During the recording of the activity of each neuron, a rabbit performed alternating (left or right side of the experimental chamber) series of instrumental behavioral acts as well as acts with a delay period before the pedals were visible behind the shutter.

We recorded single-unit activity along with electromyogram (*m. masseter pars profundus*) and the timeline of behavioral events (details in Alexandrov, Grinchenko and Jarvilehto, 1990). The rabbit's behavior was also video-recorded with the unit activity (audio-channel), the light indicators of the pedal pressing and head lowering, the counters of the cumulative number of spikes, and of time. As the animals' training (or behavioral shaping) consisted of several consecutive stages on each side of the experimental chamber (food intake from the feeder, turning head and body from the feeder, turning to the pedal, pressing the pedal, turning to the feeder), the results of these training stages were later used to divide behavior into behavioral elements with corresponding markers recorded in all sessions.

Data analysis

Each behavioral cycle on the left side of the cage was divided in accordance with the behavioral marks into five stages (behavioral acts): (1) turning a head toward a pedal; (2) approaching a pedal; (3) pressing a pedal; (4) approaching a feeder and (5) seizing food. Behavior on the right side of the cage was divided into analogous stages (acts 6-10; see Fig. 1). The following indices were selected as the characteristics of the activity of the neuron: the average frequency of spike activity in a particular act and the probability of an activation in the act. The average frequency of activity for the entire recording was calculated for each neuron. The exceeding by the frequency of the activity in one or several acts of the average frequency of the activity of a neuron over the whole period of its recording (or during the period preceding the flash) by not less than a factor of 1.5 was taken as activation (details see in Gorkin and Shevchenko, 1991).

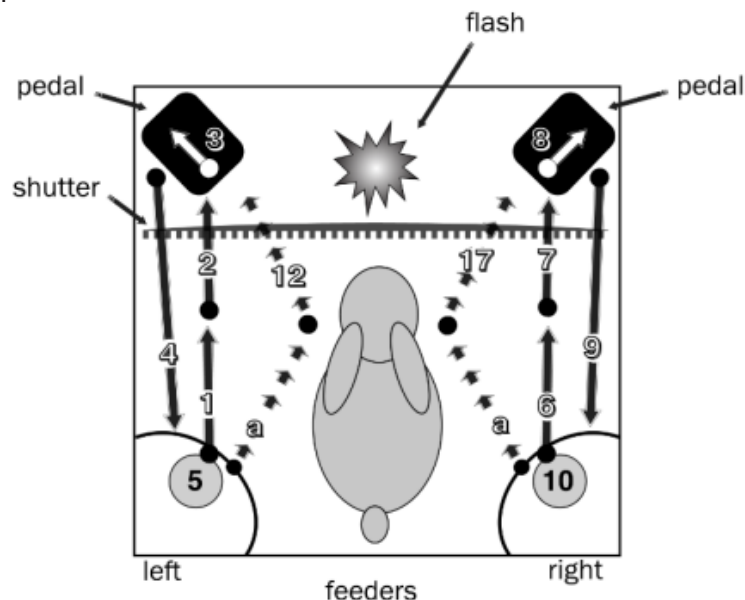


Figure 1. The experimental cage and all studied behavioral acts: 1 - turning a head from the left feeder to the left pedal; 2 - approaching the left pedal; 3 - pressing the left pedal; 4 - approaching the left feeder, 5 - food intake from the left feeder, 6 - turning a head from the right feeder to the right pedal; 7 - approaching the right pedal; 8 - pressing the right pedal; 9 - approaching the right feeder, 10 - food intake from the right feeder, a - the delay period, 12 - approaching the left pedal after the delay period, 17 - approaching the right pedal after the delay period.

In our previous studies, different types of neuronal specializations were identified in various brain areas of freely moving rabbits and rats that were performing instrumental food-acquisition behavior in an operant cage equipped with two pedals and two feeders (e.g. Alexandrov et al., 2018). Neurons could be classified in two main categories. "Narrow selective" (NS) neurons which are activated in relation to narrow range of behavioral acts of the task (i.e. approaching the feeder, taking food from the feeder, approaching the pedal and/or pressing the pedal). These behavioral acts are formed during an animal's training in the operant chamber. Their changes in activity are selectively related to a certain behavioral act, but is independent of its detailed motor execution. A neuron was considered to be specialized relative to a system of specific behavioral act if the activation in this act was observed in all cases (100% of performances of a certain act). The other category – "broadly selective" (BS) neurons. These neurons are less selective in relation to behavioral acts of the task. Their activation might be related to a certain movement (e.g. turning left or right independent of the goal of action). They are activated during an identical movement that can be performed in different behavioral contexts. Neurons that showed activation in relation to a particular movement of the body, head or lower jaw were considered to be specialized relative to the systems formed earlier in ontogeny (see in Shvyrkov, 1986, Alexandrov et al., 2000). Neurons that cannot be identified as neurons of one or the other category were named "undefined" or "unidentified", they did not show consistent activation during the given task, i.e. their specializations were unknown.

Results

A total of 356 single-unit extracellular recordings were obtained (not fewer than 50 neurons from each rabbit). From the complete sample, a total of 176 recorded in the cingulate cortex were used in the statistical analysis. The rest of the sample was eliminated because of failure to meet the inclusion criterion (i.e., stable recording during not fewer than five behavioral cycles on both sides of the experimental chamber in a control situation, and when a delay period was introduced). Approximately half of the analyzed neurons (89 neurons) had their activity specifically related to the acquired task (task-related neurons). A representative task-related neuron is on Fig. 2. The other neurons were classified as unidentified in relation to the task.

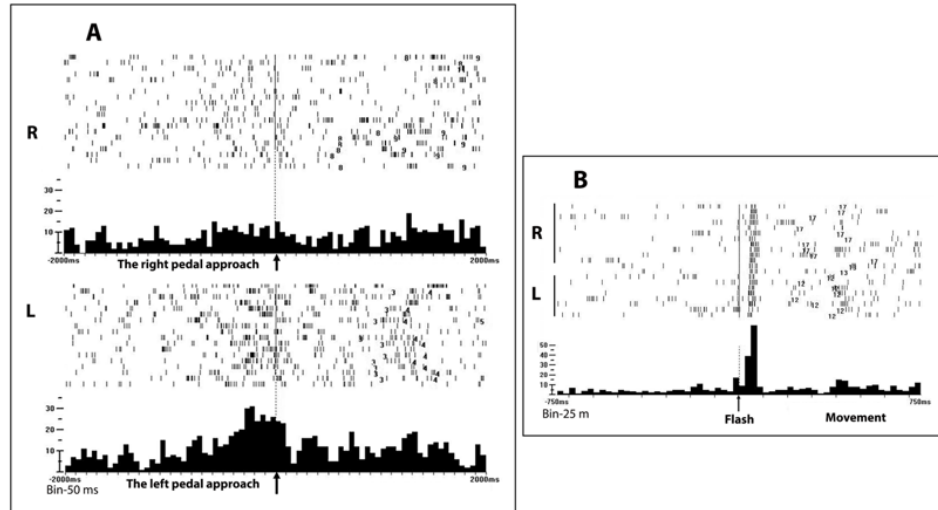


Figure 2. Activity of a representative task-related neuron specialized in relation to the left pedal approach during the instrumental behavior on both sides (A) and during the delay period (B).

Various types of neuronal activity were noticed among unidentified neurons. Neurons of one group (39%) had rare impulse activity throughout behavioral cycles (3-8 action potentials per cycle or fewer), which however unpredictably increased in some situations. Another group of neurons (23%) had evenly distributed rate of activity during behavioral cycles. Other neurons (33%) demonstrated sporadic activity, not related to behavioral acts.

Among unidentified neurons only 2.3 % (2 neurons) of cells changed their activity rate during the delay period. Both of these neurons were belonging to the group with sporadic activity, and in both of these cases activity was inhibited during the delay period.

In contrast, out of the task-related neurons 29 cells (32.6%) significantly changed their rate of

activity during the delay period. Out of them 19 neurons increased their firing rate. Among the other ten task-related cells with inhibition during the delay period were both narrow-selective neurons and broadly selective neurons (see Methods for details) in almost equal proportions. We could not find any special peculiarities in these delay-related inhibition neurons as compared to neurons with delay-related activation.

Task-related neurons we further classified into two categories: (1) NS-neurons and (2) BS-neurons (see Methods for details). The numbers of NS-neurons and BS-neurons were approximately the same: 43 and 46, respectively.

Eleven cells (26%) among NS-neurons and 11 cells (24%) among BS-neurons activated during the delay period. The mean latency of activation (maximal frequency was taken as a point of activation) after the flash during the delay period was different for NS-neurons and BS-neurons: 151.8 ± 27.6 ms for NS-neurons and 249.5 ± 31.9 ms for BS-neurons (Mann-Whitney, $p < 0.05$). As compared to NS-neurons (out of which nearly a quarter had short-latent activations) none of BS-neurons had short latency of activation – earlier than 100 ms after the flash (Fig. 3).

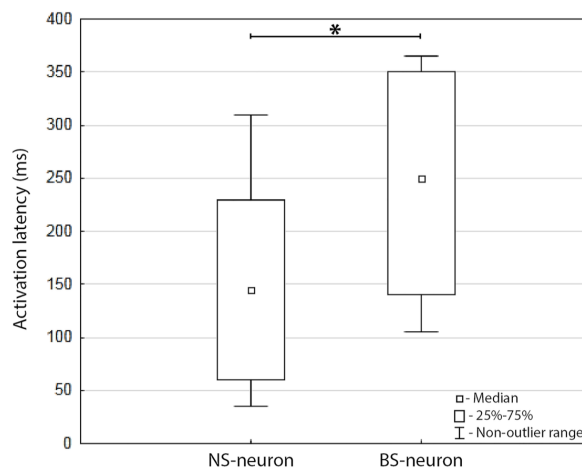


Figure 3. Neuronal activation latencies after the flash. NS – narrow selective neurons, BS – broadly selective neurons.

In addition to the acts where NS-neurons showed selective and stable activations it was noticed that NS-neurons could be activated during some behavioral acts that were not specific for them. For example, a neuron, activated during pedal-pressing, had to be activated in all acts of pedal pressing in order to be classified as narrow selective (NS-neuron) in relation to pedal-pressing. But the same “pedal” neuron could increase its firing rate during, for example, in some of the cases, feeder approaching. We counted such non-specific activations (to be counted they had to appear in at least 40% of the same acts, see details in Alexandrov et al., 2018; Sozinov, Bakhchinaa and Alexandrov, 2021) for every task-related neuron. We found that the number of non-specific activations was significantly higher for those task-related neurons that belonged to NS-neurons activated during the delay period (mean – 2.9 acts) as compared to NS-neurons that didn’t activated during the delay period (1.53 acts) or BS-neurons (2 and 1.92 acts, respectively activated and non-activated during delay periods) (Mann-Whitney, $p < 0.05$).

Discussions

In the present study we, as many others, demonstrated that animals “doing nothing” (no overt behavior present) still have their brains “full of meaning”, and that the so-called “background” activity is not “noise”, but is related to the organization of behavior (Vaadia et al., 1995; Arieli et al., 1996; Contreras et al., 2013; Kim et al., 2019). It might be suggested that spontaneous activity in the brain is its regular activity, and that ongoing spontaneous activity is modified by new experience formation (Wilson and McNaughton, 1994). The nature of such spontaneous activity is often described as elusive, but it might reflect recent experience. The brain is considered not as a passive input–output system, but as an active, projective “device” that spontaneously generates “hypotheses” and tests their adequacy (e.g. Shvyrkov, 1986; Buzsaki, 2019). It has been shown that animals’ interactions with environment enhances

similarities between spontaneous and environment-related neural activity (Berkes et al., 2011). Repeated stimulations, even in urethane-anesthetized rats, produced reoccurring of evoked unique sequential patterns of neural firing in corresponding cortices, moreover such reoccurrence requires desynchronization during stimulations (Contreras et al., 2013). Diversity of spontaneous activity patterns is generated by prefrontal cortical neurons (Dehaene and Changeux, 1997). In the present study, approximately one-third of recorded task-related neurons was activated during the delay period. The neurons whose selectivity could not be identified as related to the task did not show activations during this period. All together it implies that so called spontaneous activity should be associated with ongoing actualization of individual experience. This future-directed actualization is in line with the contemporary ideas of the proactive brain (Bar, 2009) or predictive brain (Buzsaki, 2019) or brain readiness for the future (Schurger, Pak and Roskies et al., 2021), which, in its order, can be traced back to the ideas of expected results (Anokhin, 1974) or even further (more details on the subject might be found in (Alexandrov, 2022)).

Delay periods are characterized by not only activations of narrow selective task-related neurons, but also activations of broadly selective neurons which might be related to classical "motor programs". Such results indicate that the same neurons, independent of selectivity degree, are involved in overt and covered phase of experience actualization, which might imply that decision making is embodied cognitive process. Recent data suggest that real actions and action imaging share some of the same neural substrate, which implies that conceptual knowledge is mapped within the "sensory-motor" systems or embodied in the way the organism interacts with the environment (Gallese and Lakoff, 2005). We found here that during the delay period some task-related neurons showed inhibition of activity. Thus, it can be assumed that there are at least two similarities between the compared overt and imaginary actions. The first one is the existing overlap between the sets of activated neurons in these two types of actions. The second congeniality is that they share similar characteristics of neuronal organization, which consists of opponent relationships: an activation of some neurons corresponded to an inhibition of others can be seen in both overt and covert behaviors.

Previous studies suggested that during delay periods neuronal activity is temporally organized (MacDonald et al., 2013), though it might look unclear, why some neurons fire earlier than others. We showed that task-related neurons activated in a certain order during the delay period: narrow selective neurons activated preferentially earlier as compared to neurons with less selective specializations. It was earlier shown that some neurons of motor cortex and in prefrontal cortex were modulated early in the delay period while other neurons of the same areas were modulated in a persistent manner over the duration of the delay period, moreover delay-related modulations started earlier in motor cortex than in the prefrontal cortex (Narayanan and Laubach, 2009). It was also shown (Thura and Cisek, 2014) that approximately 280 ms before movement onset, premotor cortical activity tuned to the selected target reached a consistent peak while motor cortex activity tuned to the unselected target was suppressed, which might reflect the resolution of a competition between the potential behavioral acts during decision making. In this work we showed that narrow selective neurons fire before broadly selective neurons during delay periods. If we considered developmental history of these neurons, we could infer that broadly selective neurons acquire their specializations earlier in ontogenesis as compared to narrow selective neurons. Thus, less selective neurons are active simultaneously with different sets of neurons, these neurons are shared portions of many neuronal groups. During mental rehearsal activity of the more selective neurons «drives» activation of less selective neurons. It was shown earlier that broadly selective neurons have different activity patterns dependent on the neuronal set they are in accordance (see details in Alexandrov et al., 2000, Alexandrov et al., 2018). Thus, less selective neurons are active simultaneously with different sets of neurons, these neurons are shared portions of many neuronal groups. During mental rehearsal activity of the more selective neurons «drives» activation of less selective neurons. It was shown earlier that broadly selective neurons have different activity patterns dependent on the neuronal set they are in accordance (details see in e.g. Alexandrov, 2008). It might be suggested that in order to fulfill this accordance narrow selective neurons appear to have more cases of non-specific activity (which implies more functional connections) as we showed in this work. We also found that neurons with the higher number of functional connections fire earlier than others. This finding might be related to the idea of "hub" neurons (e.g., Cossart, 2014), which have more functional connections and might have a higher number of spontaneous firings.

Conclusions

Our theoretical framework suggest that neurons are specialized in relation to not the function of decision making, perception or motor programs but the systemic functions, i.e., functional systems formed for reaching different adaptive individual results in the environment (see, e.g., Anokhin, 1974; Alexandrov, 2008, 2022; Alexandrov et al., 2018). Hence memory content that may be used at any stage of behavior preparation, is memory about all behavioral acts formed during individual history. Systemically specialized neurons underly these memories. Memory actualization is, in turn, activations of those neurons. The results described in this article showed that mental rehearsal during delay periods demonstrated features of embodiment – activity of the same neurons that are used during overt movements. Moreover, this neuronal activity is temporally organized in a specific way which might be considered as mechanisms of embodiment. Neuronal activity sequence during the delay period, used for decision making, depends on the role of neuron in overt behavior. In summary, we found a specific pattern of neuronal activity during delay period related to embodied decision making.

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Conflict of interests

The authors declare no conflict of interest.

References

- Alexandrov, Y. I. (2008). How we fragment the world: the view from inside versus the view from outside. *Social Science Information*, 47(3), 419–457. <https://doi.org/10.1177/0539018408092580>
- Alexandrov, Y. I. (2022). "Chapter 3 Systemic Psychophysiology". In: Forsythe C. (ed.). *Russian Cognitive Neuroscience: Historical and Cultural Context*. Leiden, The Netherlands: Brill. P. 56-86. https://doi.org/10.1163/9789004505667_004
- Alexandrov, Y. I., Grinchenko, Y. V., & Jarvilehto, T. (1990). Change in the pattern of behavioural specialization of neurons in the motor cortex of the rabbit following lesion of the visual cortex. *Acta physiologica scandinavica*, 139(1-2), 371-385. <https://doi.org/10.1111/j.1748-1716.1990.tb08936.x>
- Alexandrov, Y. I., Sozinov, A. A., Svarnik, O. E., Gorkin, A. G., Kuzina, E. A., & Gavrilo, V. V. (2018). Neuronal bases of systemic organization of behavior. In *Systems Neuroscience* (pp. 1-33). Springer, Cham. https://doi.org/10.1007/978-3-319-94593-4_1
- Alexandrov, Yu.I., Grechenko, T.N., Gavrilo, V.V., Gorkin, A.G., Shevchenko, D.G., Grinchenko, Y.V., et al. (2000). Formation and realization of individual experience in humans and animals: a psychophysiological approach. In: R. Miller, A.M. Ivanitsky & P.M. Balaban (eds) *Conceptual Advances in Brain Research, Complex Brain Functions Conceptual Advances in Russian Neuroscience, Vol. 2*, pp. 181-200. Amsterdam: Harwood Academic Publishers.
- Andersen, R. A., & Cui, H. (2009). Intention, action planning, and decision making in parietal-frontal circuits. *Neuron*, 63(5), 568-583. <https://doi.org/10.1016/j.neuron.2009.08.028>
- Anokhin, P. K. (1974). *Biology and Neurophysiology of Conditioned Reflex and Its Role in Adaptive Behavior*, 1st ed. Oxford: Pergamon Press.
- Arieli, A., Sterkin, A., Grinvald, A., & Aertsen, A. D. (1996). Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. *Science*, 273(5283), 1868-1871. <https://doi.org/10.1126/science.273.5283.1868>
- Bar, M. (2009). The proactive brain: memory for predictions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1521), 1235-1243. <https://doi.org/10.1098/rstb.2008.0310>
- Berkes, P., Orbán, G., Lengyel, M., & Fiser, J. (2011). Spontaneous cortical activity reveals hallmarks of an optimal internal model of the environment. *Science*, 331(6013), 83-87. <https://doi.org/10.1126/science.1195870>
- Bisley, J. W., Zaksas, D., Droll, J. A., & Pasternak, T. (2004). Activity of neurons in cortical area MT during a memory for motion task. *Journal of neurophysiology*, 91(1), 286-300. <https://doi.org/10.1152/jn.00870.2003>
- Buzsaki G. (2019). *The Brain from Inside Out*. New York: Oxford University Press.
- Catanese, J., Cerasti, E., Zugaro, M., Viggiano, A., & Wiener, S. I. (2012). Dynamics of decision-related activity in hippocampus. *Hippocampus*, 22(9), 1901-1911. <https://doi.org/10.1002/hipo.22025>
- Changeux, J. P., & Dehaene, S. (1989). Neuronal models of cognitive functions. *Cognition*, 33(1-2), 63-109. [https://doi.org/10.1016/0010-0277\(89\)90006-1](https://doi.org/10.1016/0010-0277(89)90006-1)
- Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Ryu, S. I., & Shenoy, K. V. (2010). Cortical preparatory activity: representation of movement or first cog in a dynamical machine?. *Neuron*, 68(3), 387-400. <https://doi.org/10.1016/j.neuron.2010.09.015>
- Cisek, P., & Kalaska, J. F. (2004). Neural correlates of mental rehearsal in dorsal premotor cortex. *Nature*, 431(7011), 993-996. <https://doi.org/10.1038/nature03005>
- Clement, D. (1996). *Kinds of Minds: Toward an Understanding of Consciousness*. Basic Books.

- Contreras, E. J. B., Schjetnan, A. G. P., Muhammad, A., Bartho, P., McNaughton, B. L., Kolb, B., ... & Luczak, A. (2013). Formation and reverberation of sequential neural activity patterns evoked by sensory stimulation are enhanced during cortical desynchronization. *Neuron*, 79(3), 555-566. <https://doi.org/10.1016/j.neuron.2013.06.013>
- Cossart, R. (2014). Operational hub cells: a morpho-physiologically diverse class of GABAergic neurons united by a common function. *Current opinion in neurobiology*, 26, 51-56. <https://doi.org/10.1016/j.conb.2013.12.002>
- Crammond, D. J., & Kalaska, J. F. (2000). Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *Journal of neurophysiology*, 84(2), 986-1005. <https://doi.org/10.1152/jn.2000.84.2.986>
- Dehaene, S., & Changeux, J. P. (1997). A hierarchical neuronal network for planning behavior. *Proceedings of the National Academy of Sciences*, 94(24), 13293-13298. <https://doi.org/10.1073/pnas.94.24.13293>
- Dennet, D.C. (1996). *Kinds of minds: Toward an understanding of consciousness*. New York: Harper Collins Publishers.
- Ferster, D. (1996). Is neural noise just a nuisance?. *Science*, 273(5283), 1812-1812. <https://doi.org/10.1126/science.273.5283.1812>
- Foster, D. J., & Wilson, M. A. (2006). Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature*, 440(7084), 680-683. <https://doi.org/10.1038/nature04587>
- Freedman, D. J., & Assad, J. A. (2011). A proposed common neural mechanism for categorization and perceptual decisions. *Nature neuroscience*, 14(2), 143-146. <https://doi.org/10.1038/nn.2740>
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, 22, 455-479. <https://doi.org/10.1080/02643290442000310>
- Gheidi, A., Satvat, E., & Marrone, D. F. (2012). Experience-dependent recruitment of Arc expression in multiple systems during rest. *Journal of Neuroscience Research*, 90(9), 1820-1829. <https://doi.org/10.1002/jnr.23057>
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual review of neuroscience*, 30(1), 535-574. <https://doi.org/10.1146/annurev.neuro.29.051605.113038>
- Gorkin, A. G., & Shevchenko, D. G. (1991). Stability of the behavioral specialization of neurons. *Neuroscience and behavioral physiology*, 21(3), 222-229. <https://doi.org/10.1007/BF01191659>
- Ingram, T. G., Krautner, S. N., Solomon, J. P., Westwood, D. A., & Boe, S. G. (2016). Skill acquisition via motor imagery relies on both motor and perceptual learning. *Behavioral Neuroscience*, 130(2), 252. <https://doi.org/10.1037/bne0000126>
- Kim, K., Ladenbauer, J., Babo-Rebelo, M., Buot, A., Lehongre, K., Adam, C., ... & Tallon-Baudry, C. (2019). Resting-state neural firing rate is linked to cardiac-cycle duration in the human cingulate and parahippocampal cortices. *Journal of Neuroscience*, 39(19), 3676-3686. <https://doi.org/10.1523/JNEUROSCI.2291-18.2019>
- MacDonald, C. J., Carrow, S., Place, R., & Eichenbaum, H. (2013). Distinct hippocampal time cell sequences represent odor memories in immobilized rats. *Journal of Neuroscience*, 33(36), 14607-14616. <https://doi.org/10.1523/JNEUROSCI.1537-13.2013>
- Murakami, M., & Mainen, Z. F. (2015). Preparing and selecting actions with neural populations: toward cortical circuit mechanisms. *Current opinion in neurobiology*, 33, 40-46. <https://doi.org/10.1016/j.conb.2015.01.005>
- Narayanan, N. S., & Laubach, M. (2009). Delay activity in rodent frontal cortex during a simple reaction time task. *Journal of neurophysiology*, 101(6), 2859-2871. <https://doi.org/10.1152/jn.90615.2008>
- O'Neill, J., Pleydell-Bouverie, B., Dupret, D., & Csicsvari, J. (2010). Play it again: reactivation of waking experience and memory. *Trends in neurosciences*, 33(5), 220-229. <https://doi.org/10.1016/j.tins.2010.01.006>
- Park, I. M., Meister, M. L., Huk, A. C., & Pillow, J. W. (2014). Encoding and decoding in parietal cortex during sensorimotor decision-making. *Nature neuroscience*, 17(10), 1395-1403. <https://doi.org/10.1038/nn.3800>
- Rushworth, M. F. S., Walton, M. E., Kennerley, S. W., & Bannerman, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in cognitive sciences*, 8(9), 410-417. <https://doi.org/10.1016/j.tics.2004.07.009>
- Sauvage, C., De Greef, N., Manto, M., Jissendi, P., Nioche, C., & Habas, C. (2015). Reorganization of large-scale cognitive networks during automation of imagination of a complex sequential movement. *Journal of neuroradiology*, 42(2), 115-125. <https://doi.org/10.1016/j.neurad.2014.04.001>
- Schurger, A., Pak, J., & Roskies, A. L. (2021). What is the readiness potential?. *Trends in cognitive sciences*, 25(7), 558-570. <https://doi.org/10.1016/j.tics.2021.04.001>
- Shvyrkov, V. B. (1986). Behavioral specialization of neurons and the system-selection hypothesis of learning. In: F. Klix & H. Hagendorf (eds) *Human Memory and Cognitive Capabilities*, pp. 599-611. Amsterdam: Elsevier.
- Singer, A. C., Carr, M. F., Karlsson, M. P., & Frank, L. M. (2013). Hippocampal SWR activity predicts correct decisions during the initial learning of an alternation task. *Neuron*, 77(6), 1163-1173. <https://doi.org/10.1016/j.neuron.2013.01.027>
- Sozinov, A. A., Bakhchina, A. V., & Alexandrov, Y. I. (2021). The Way of Learning Preserved in The Structure of Individual Experience Shapes Task-Switching: Implications for Neuroscience and Education. *International Journal of Cognitive Research in Science, Engineering and Education:(IJCRSEE)*, 9(2), 291-299. <https://doi.org/10.23947/2334-8496-2021-9-2-291-299>
- Svarnik, O. E., Alexandrov, Y. I., Gavrilov, V. V., Grinchenko, Y. V., & Anokhin, K. V. (2005). Fos expression and task-related neuronal activity in rat cerebral cortex after instrumental learning. *Neuroscience*, 136(1), 33-42. <https://doi.org/10.1016/j.neuroscience.2005.07.038>
- Tervo, D. G., Proskurin, M., Manakov, M., Kabra, M., Vollmer, A., Branson, K., & Karpova, A. Y. (2014). Behavioral variability through stochastic choice and its gating by anterior cingulate cortex. *Cell*, 159(1), 21-32. <https://doi.org/10.1016/j.cell.2014.08.037>
- Thura, D., & Cisek, P. (2014). Deliberation and commitment in the premotor and primary motor cortex during dynamic decision making. *Neuron*, 81(6), 1401-1416. <https://doi.org/10.1016/j.neuron.2014.01.031>
- Vaadia, E., Haalman, I., Abeles, M., Bergman, H., Prut, Y., Slovin, H., & Aertsen, A. M. H. J. (1995). Dynamics of neuronal interactions in monkey cortex in relation to behavioural events. *Nature*, 373(6514), 515-518. <https://doi.org/10.1038/373515a0>
- van der Meer, M.A., Redish, A.D. (2010). Expectancies in decision making, reinforcement learning, and ventral striatum. *Frontiers in Neuroscience*, 15, 6. <https://doi.org/10.3389/neuro.01.006.2010>
- Vann, S. D., Aggleton, J. P., & Maguire, E. A. (2009). What does the retrosplenial cortex do?. *Nature reviews neuroscience*, 10(11), 792-802. <https://doi.org/10.1038/nrn2733>

- Viard, A., Chételat, G., Lebreton, K., Desgranges, B., Landeau, B., de La Sayette, V., ... & Piolino, P. (2011). Mental time travel into the past and the future in healthy aged adults: an fMRI study. *Brain and cognition*, 75(1), 1-9. <https://doi.org/10.1016/j.bandc.2010.10.009>
- Vogt, B. A. (2016). Cytoarchitecture and neurocytology of rabbit cingulate cortex. *Brain Structure and Function*, 221(7), 3571-3589. <https://doi.org/10.1007/s00429-015-1120-x>
- Walton, M. E., Devlin, J. T., & Rushworth, M. F. (2004). Interactions between decision making and performance monitoring within prefrontal cortex. *Nature neuroscience*, 7(11), 1259-1265. <https://doi.org/10.1038/nn1339>
- Whittingstall, K., Bernier, M., Houde, J. C., Fortin, D., & Descoteaux, M. (2014). Structural network underlying visuospatial imagery in humans. *Cortex*, 56, 85-98. <https://doi.org/10.1016/j.cortex.2013.02.004>
- Wilson, M. A., & McNaughton, B. L. (1994). Reactivation of hippocampal ensemble memories during sleep. *Science*, 265(5172), 676-679. <https://doi.org/10.1126/science.8036517>