Charles University in Prague

Faculty of Science

Department of Philosophy and History of Science

Theoretical and Evolutionary Biology

Andres Kurismaa, M.Sc.

Towards an Ecology of the Brain:

Reassessing the Dominant as a Paradigm of Organismic and Anthropological Physiology

Doctoral thesis

Supervisor:
doc. Mgr. Karel Kleisner PhD.
Prague, 2019

Declaration:

I hereby declare that this thesis is the result of my own work and effort. The literature is properly cited. This thesis has not been presented, nor is it being presented, either wholly or in part, for any other degree in this or any other institution.

In Prague, July 12, 2019   **Andres Kurismaa, M.Sc. ……………………………………….**

ACKNOWLEDGEMENT:

ABSTRACT

This thesis presents a series of inter-related case studies (Kurismaa 2015; Kurismaa and Pavlova 2016; Pavlova, Berlov and Kurismaa 2017) aiming to reexamine, from modern perspectives, one of the most significant and integrative approaches to neurophysiology in the 20-th century – the study of the dominant (учение о доминанте) by the physiologist acad. A.A. Ukhtomsky (1875–1942) and his scientific school. Although recognized as a critical contribution and framework for organism-centered study of physiology, knowledge of this school has remained minimal in the West, and to this day, almost entirely unexplored for its prospects of integration and interrelation with respective foreign research programs in biology and neuroscience, both past and present.

In recent years, and partly on the initiative of the present author, some of the first attempts have been made to overcome these limitations, and to more systematically address the legacy of Ukhtomsky's school from modern perspectives in Western science (Nadin 2015). The present thesis, growing out from these efforts, contributes further materials to such comparative and methodological investigation. It aims specifically to clarify the modern status and significance of the dominant framework as an integrative and organismic paradigm for neuroscientific research, and to show its potentially wide implications for human neuroscience in particular, as a socially and culturally (anthropologically) oriented discipline.

Focused on the questions of historicity and temporal variability (process dynamics, chronogenic variation) as explanatory tools and concepts, the presented case studies touch upon theoretical problems ranging from basic homeostasis at the cellular and network levels, to problems of human labor and social neuroscience. All these applications are shown to derive from the basic physiological paradigm of the dominant, demonstrating its continued significance and integrative potential in the context of modern research, both fundamental and applied.

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2. Kurismaa, A., & Pavlova, L. P. (2016). The dominant as a model of chronogenic change: The relevance of AA Ukhtomsky's and LS Vygotsky's traditions for systemic cognitive studies. In: *Centrality of History for Theory Construction in Psychology* (pp. 125-149). Springer, Cham.
3. Pavlova, L. P., Berlov, D. N., & Kurismaa, A. (2018). Dominant and opponent relations in cortical function: An EEG study of exam performance and stress. *AIMS Neuroscience*, 5(1): 32-55.
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1. Introduction

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INTRODUCTION

1. The paradigm of the dominant – historical background and current status

This thesis presents a series of inter-related case studies aiming to reexamine, from modern perspectives, one of the most significant and integrative approaches to neurophysiology in the 20-th century – the study of the dominant (учение о доминанте) by the physiologist acad. Aleksei A. Ukhtomsky (1875–1942), and his scientific school (Merkulov 1960; Airapetyants 1967; Batuev et al 1990; Nozdrachev and Samoilova 2000; Kurismaa 2015; Pavlova 2017). Although recognized as a critical contribution and framework for the organism-centered study of neurophysiology (Batuev et al 1990; Nadin 2015), knowledge of this school has remained minimal in the West, and to this day, almost entirely unexplored for its prospects of integration and interrelation with respective foreign research programs in biology and neuroscience, both past and present. Some of the circumstances for this will be addressed further below.

Only in recent years, partly on the initiative of the present author, were some of the first attempts made to more systematically address the legacy of Ukhtomsky's school from modern perspectives in Western research (Kurismaa 2015; Kazansky 2015). This has allowed to recognize its lasting interest for fundamental science, and to critically assess its contributions in methodological and historical light. The present thesis, growing out from these efforts, contributes further materials to these comparative and methodological investigations. At the same time, its emphasis proceeds from the more retrospective and conceptual aspects already addressed in recent works (Zueva and Zuev 2015; Sokolova 2010, 2015; Nadin 2015), to include specific case studies and questions relevant for current research in several areas of neuroscience and theoretical works. This allows to formulate the modern backgrounds for understanding the dominant as a scientific framework, and its central methodological tenets in the perspective of time.

With the concept of the dominant, first explicated in a series of papers in the 1920-s (republished in Ukhtomsky 1950-1962, 1966, 1978), Ukhtomsky and colleagues sought to investigate from new perspectives a central problem of neurophysiology – how the integration of organismic responses depends on dynamic changes of excitability in particular brain areas, and functional modifications in inter-central connectivity. This concerns specifically the formation of behavioral or other physiological reactions by means of the temporary exclusion of functionally competing neural centers and pathways via their lateral inhibition by the dominant state. In this context, a dominant constellation of brain centers can be defined as an object of physiological study, presenting a complex of symptoms with definite properties – such as a sufficiently stable level of increased excitability, the ability to accumulate and sum incoming excitations from distant brain regions (including those normally not having synergic or compatible effects), the dominant's reaction-inertia, and ability to inhibit the excitability of other brain centers – the functions of which are widely suppressed or temporarily coopted in line with the dominant focus (Ukhtomsky 1966).

In the 1920-s, early experiments had already demonstrated that in diverse model systems, ranging from mammals to cold-blooded vertebrates (e.g., frogs) and invertebrates (the pond snail L. stagnalis), such dominant foci can be set up through diverse means, and lead to marked modifications in patterns of inter-central innervation and brain function (Ukhtomsky 1966). This lend support to viewing physiological dominants as potent integrators of nervous and organismic activity, with possibly universal neurophysiological significance for the regulation of functions. Indeed, respective self-corroborating networks or constellations with dominant properties could be set up on various levels

of the brain, and under the influence of distinct pharmacological, mechanical, or endogenous physiological (e.g., hormonal) agents. As one of its most remarkable results, this line of works showed not only that identical external stimuli may evoke altered reflex reactions in the same animal on the background of various dominants, but furthermore, that even normally antagonistic pathways and competing stimuli may come to reinforce the dominant reaction once it's sufficiently stabilized and established in the nervous system (Ukhtomsky 1966, 1978). Some of the earliest demonstrations of this were given in the classical studies of Ukhtomsky (Ukhtomsky 1911). By stimulating electrically the motor cortex of experimental animals, it was shown that the limb movements normally evoked by this stimulation may be inhibited or blocked when the animal is engaged in a particular adaptive act, such as swallowing or defecating, and furthermore, that these ongoing "dominant" reactions may be reinforced from motor zones normally responsible for moving the extremities. As the adaptive act is concluded, the normal patterns of neuro-motor responsiveness and functional innervation are restored in the organism (Ukhtomsky 1911). In this context, Ukhtomsky refers to the dominant as a "disruptor" of equilibrium in inter-central relations, and sees it as a general operating principle of nervous centeres under normal conditions of life – subject to organisms' constantly changing needs and actions (Ukhtomsky 1966). It should be noted that to this day, the nature of respective neural mechanisms remains largely open, and its particular manifestations (e.g., lateral inhibition) are the object of many studies, particularly by electroencephalographic (EEG) methods (see ch. 2 and 3 of the present thesis; cf. Jensen and Mazaheri 2010; Klimesch 2012; Pavlova 2017).

On the other hand, besides representing an object of immediate physiological investigation with particular symptoms and properties, the dominant as a research paradigm represents first of all a specific methodological and conceptual approach to neurophysiology and biology. It's in this perspective that it obtains its specific meaning and significance also for modern studies. Indeed, what remains striking about the initial formulations of Ukhtomsky already in the 1920-s is their theoretical and methodological nature. This remains not only contemporary, but may well speak to the requirements and challenges of future research paradigms dealing with complex dynamic aspects of biology and neuroscience – including the physiologically realistic modelling of irreversible and non-linear processes, autocatalytic and negentropic phenomena, critical stability, stochastic facilitation, and related problems (Igamberdiev 2012; McDonnell and Ward 2011; Shew and Plenz 2013). All of these aspects highlight the historically conditioned, emergent or self-organizing properties of living systems – and all of them were in various ways prefigured in the methodology of the dominant as an organismic physiological, and indeed anthropological research paradigm, as shown further below (section 3, pp. 12–15).

In this context, the simpler mechanistic models of the living are by logical necessity subordinated to a secondary and derivative position with respect to the processes by which such mechanisms are constantly assembled, re-assembled, and dismantled in the fabric of life (Ukhtomsky 1966: 149). Although such constructive focus on living systems as self-fabricating and self-assembling entities has gained a strong foundation in subsequent schools of theoretical biology in the West (Pattee and Rączaszek-Leonardi 2012; Rosen 1991, 2000, 2012; Maturana and Varela 1987, 1991; Hofmeyr 2017), it's remarkable how little influence these ideas appear to have had in neuroscience and -physiology up until the present (Anderson et al 2012; Dotov 2014). It is in this context that the unique position of the dominant can be situated theoretically and historically.

Indeed, there is little doubt that among the fields standing to benefit most from the investigation of related complex and organizational properties, brain research may stand out specifically for its highly dynamic and complex subjects – related to such essential problems as the time-varying organization of functions, their mutual interference and integration, as well compensation in case of pathological

processes or disturbances. In all these cases, the dominant has provided important sources for neurophysiological research in the USSR (Airapetyants 1967; Kositskiy and Smirnov 1970; Batuev et al 1990; Ilyukhina 2015; Pavlova 2017).

Below (section 3), it's proposed that the respective methodological aspects of the dominant can be best highlighted by drawing a heuristic distinction between the representational (descriptive, informational), mechanistic (causal analytic), and organizational (relational organismic) levels of modelling in biosystems and neuroscience. This allows to highlight the extent to which the significant progress, made at the levels of representational and mechanistic modelling in the intervening time, appears to contrast with the relative lack of advances regarding the organizational study of neural systems. This includes particularly their study in historical and temporal-developmental terms, with a focus on the normal variability of functions and their dynamics in biological time. These were the precise aspects at the focus of the dominant framework, as well as related physiological approaches in the USSR (Anokhin 1974; Bernstein 1967; Whiting 1983). In this context, the idea of historicity will be highlighted in more detail (section 3), as perhaps one of the most distinctive aspects of the dominant approach to the organization of functions and physiological processes.

However, besides these general biological and neurophysiological features, there are further aspects of the dominant paradigm which stand out in the modern light. These address specifically the fields of human and social neuroscience, including their cultural-historical and anthropological dimensions (Wolfe 2009). Indeed, approaching these areas of functioning may require particular methods of psycho- and neurophysiological study (Pavlova and Romanenko 1988; Pavlova 2017), where the general emphasis on history as an explanatory concept in physiology must attain a further, cultural-historical meaning. This is specifically expressed in the semiotically mediated aspects of human brain functions – including their dependence on verbal self-regulation and symbolic communication, as well as complex labor and tool-use in social conditions. The fact that the dominant framework laid the foundations of theoretical labor physiology in the USSR is significant in this context (Zolina and Izmerov 1983), and reflects its orientation to problems that go beyond general physiology to encompass the realm of specifically human activities – including their marked individual variability, structural complexity, and social settings. All of these may demand appropriate methodological tools and methods of study, as considered specifically in the dominant framework (Airapetyants 1967; Batuev et al 1990; Pavlova 2017).

Also in Western research traditions, related problems have been long recognized. This has found particular attention in early works associated with the schools of "anthropological physiology" and medicine (Fagot-Largeault 2009; Danzer 2011; von Weizsäcker 1968; Buytendijk 1974). By realizing that new frameworks and physiological methods may be needed to more successfully apply them to the human realm, these works show aspirations that are clearly shared with that of Ukhtomsky's dominant as a complex biosocial paradigm (Sokolova 2010; Pavlova 2017). However, as will be considered below, the critical contribution and difference of the latter appears to be its distinct methodological orientation, expressed already in the non-mechanistic and dynamic analysis of simpler biological systems, and their comprehensive experimental studies from alternative, integrative physiological perspectives. These do not raise anthropological problems per se, but may be crucial for the latter's investigation and resolution from new viewpoints – including in the analyses of human higher cortical functions, as discussed in this thesis (ch. 2 and 3). Given the widely acknowledged anthropological interest of the dominant paradigm (Tkachenko et al 2018; Sokolova 2010), speaking of anthropological physiology may indeed seem most appropriate in this context, and the dominant seen as an autonomous framework for its study – in many aspects relatable to, but also distinct from its historical traditions and counterparts in the West (Danzer 2011; Wiggins and Schwartz 2013;

Duncker and Prieß 2006). Although not considered in more detail in the included chapters, this may prove important in the future for integrating the dominant with relevant approaches to philosophical biology and anthropology in the West, and pursuing related lines of holistic research further.

This would be particularly relevant also as the dominant framework has remained paradoxically little known in the West, regardless of its fundamental contributions to physiology and neuroscience. Historically, this omission may appear as one of the many side-results of the wider scientific isolation and ideological polarization characterizing 20-th century social and intellectual history. On this background, research programs in the USSR and the West developed largely autonomously in many areas, and came to possess marked differences in terms of basic methodology and philosophical orientation (Graham 1987; Toades 1989), particularly in the life sciences and neurophysiology (Graham 1987; Mecacci 1979). On the other hand, it's to be noted that this divergence is not a late or arbitrary appearance, but appears to follow from significantly longer and larger scientific trends, going back at least to the works of the St. Petersburg school of physiology in the late 19-th century – including not only the works of Ukhtomsky's own teacher, the physiologist Nikolai E. Wedensky (1852–1922), but also the latter's teacher, the "father of Russian physiology" Ivan M. Sechenov's legacy (1829–1905) (Arshavsky 1975; Nozdrachev and Samoilova 2000; Grigoriev and Grigorian 2007). The distinctly organismic and evolutionary style of thinking appearing in these pioneering neurophysiological and theoretical works seems to remain exceptional and largely unparalleled among all known, major physiological schools of the 20-th century (Arshavsky 1975) – and this characterization appears to apply well up to the present time. Although highlighted by some of the most outstanding neuroscientists of the 20-th century, including Karl H. Pribram (1971), it's perhaps less surprising therefore that the dominant paradigm has remained almost inaccessible and untranslated to this day – including the fundamental volumes of Ukhtomsky's collected works (Ukhtomsky 1950–1962), and his programmatic papers on the dominant (Ukhtomsky 1966, 1978). Although to a lesser extent, the same limitations hold true for many relevant and closely related works (e.g., by the physiologists N.A. Bernstein and P.K. Anokhin, noted below).

In the following, the methodological and theoretical aspects of the dominant as a scientific paradigm will be addressed in more detail, after the contributions of the individual chapters have been outlined. Detailed looks at the biographic and historiographic aspects Ukhtomsky's life, humanistic legacy, and scientific school are available elsewhere, and go beyond the focus of the present thesis (cf. Nozdrachev and Samoilova 2000; Sokolova 2015; Reznik 2015).[1]

2. Chapter outlines and current relevance

Regarding the designation of Ukhtomsky's approach and school, various terms have been employed, such as "complex" and "biosocial" science (Sokolova 2010), in addition to the more general qualifiers of systemic and integrative physiology (Pavlova and Romanenko 1988; Pavlova 2017). Settling for a particular term is not an easy task, considering the associations these evoke in the modern context, where a variety of similar labels are used to designate other approaches and traditions, not related to

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[1] Indeed, the wide-ranging humanistic aspects of Ukhtomsky's legacy that could not be published in the USSR have been investigated by numerous authors since their appearance in recent decades (Sokolova 2010; Zueva and Zuev 2015; Reznik 2015), including his writings and personal communications on philosophical, ethical, anthropological, and religious topics (Ukhtomsky 1996, 1997, 2001). These are important for assessing the wider intellectual and historical background from which the dominant paradigm emerged (Zueva and Zuev 2015), and also for relating its anthropological and philosophical basis to those of Western traditions in theoretical biology, medicine, and anthropology in the future.

the Russian and USSR ones. In the context of more recent works, direct parallels have been sought between these Russian/USSR traditions and certain schools of Western theoretical biology. In particular, these have focused on the traditions of relational and anticipatory biology laid down in the fundamental works of Rosen (2012), and subsequent allied ideas and developments in cognitive science (Nadin 1991). On the other hand, such theoretical parallels, existing and extending over broad historical periods and transformations, must necessarily raise questions – this particularly when their potential significance is entertained for modern science. How to explain such profound discontinuities in the development of ideas, and between the scientific traditions in which they evolved?

No matter how historians or philosophers of science may answer this question, it's a fact that from recent works, numerous references may be drawn to fundamental advances that directly confirm predictions of the early physiological schools in question. This concerns most notably the traditions of N.A. Bernstein (1896–1966) and P.K. Anokhin (1898–1974). Both schools are closely associated with Ukhtomsky's teaching, and elaborated on its key ideas, specifically the notion of (dominants as) "functional organs" – systems with distributed anatomical localization, but united or coordinated effects in the behaving organism. With reference to Bernstein's work in motor control, it was recently concluded that the main lesson of a project, leading to the construction of the world's fastest walking robot at the time, was that the nested loop design first proposed by Bernstein more than 70 years ago "worked and was efficient".[2] With regard to P.K. Anokhin's functional systems theory (explicitly building upon Ukhtomsky's dominant), one of its key predictions regarding the theoretical basis of single cell neurophysiology has been finally reconfirmed in the last years (Sardi et al 2017; Vardi et al 2017), with rigorous demonstrations now showing that in single neurons, the processing of incoming synaptic signals may occur in a highly selective and constrained manner, without the possibility of summating or integrating their effects across wider areas of cell membranes. This conclusion, which was predicted and substantiated in extensive detail by Anokhin and colleagues already in the late 1960-s and early 1970-s (cf. Anokhin 1974, 1984), challenges some of the most fundamental notions of cellular neuroscience and biophysical modelling, upon which nearly 100 years of experimental and theoretical work has been carried out in areas that are foundational for neuroscience. The comments by the authors of these recent studies (Sardi et al 2017; Vardi et al 2017) are telling in this regard: "We reached this conclusion [of non-isotropic integration] using a new experimental setup, but in principle these results could have been discovered using technology that has existed since the 1980s. The belief that has been rooted in the scientific world for 100 years resulted in this delay" (I. Kanter and colleagues).[3]

In the present thesis, several lines of related evidence are considered from the perspective of Ukhtomsky's paradigm of the dominant and its subsequent developments. As shown through a number of case studies, these appear to speak of similar historical paradoxes and parallels as noted above. This may call for renewed assessments of this tradition, both in terms of basic physiological theory and its more applied results. Respective case studies are briefly outlined below.

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[2] "Roboticists are using the lessons of a 1930s human physiologist to build the world's fastest walking robot". BBC News, Technology, 12 July 07 (http://news.bbc.co.uk/2/mobile/technology/6291746.stm) [Retrieved 11.07.2019].

[3] "Physicists Negate Century-Old Assumption Regarding Neurons and Brain Activity". Bar-Ilan University press statement, 2017-12-21. Cf. https://www.sciencealert.com/physicists-overturn-old-theory-spatial-summation-brain-cells [Retrieved 11.07.2019]. Considering the scope of social investment in neuroscience, involving multi-billion dollar projects and industrial-scale research programs, estimating the approximate costs of such theoretical omissions may be a worthwhile future task.

In chapter one, attention is drawn to the fact that in current neuroscience, more intensive and theoretically guided studies on neuronal homeostasis and related problems have emerged only in recent decades. At the same time, in Russia and USSR, similar research problems appear to have a significantly longer, and so far still largely unexplored history in fundamental neuroscience and neurophysiology. It is shown that in the school of Ukhtomsky-Wedensky, large-scale investigations into the homeostatic regulation of excitable structures goes back as far as the late 19-th century. Theoretically and methodologically, this program constituted an autonomous and distinct approach to physiology and neurophysiology that not only anticipated modern research, but remains original in its focus and concepts. Indeed, in Western research at the time or now, the Ukhtomsky-Wedensky line of studies appears to have no theoretical analogue or parallel, as problems related to the homeostatic modulation and reconfiguration of neural activity and networks have emerged only very recently (Marder and Tang 2010), and with main reference to specific, slower signaling systems and pathways (e.g., dynamic effects of neuromodulatory substances and receptor systems). While bringing about significant changes in the study of neural networks, including the homeostatic variability of their mechanisms and effects in time, it may be noted that the temporal scales and signaling processes these involve are often hard to correlate with immediate behavioral and cognitive effects, including specifically the large-scale, rapidly propagating excitability changes these imply throughout the neuraxis in a behaving organism (e.g., the instances of behavioral dominance cited above, pp. 2).

On the other hand, these were precisely the main questions of the dominant framework, as part of which several integrative or organismic approaches were proposed to the homeostatic and anticipatory regulation of neural excitability. Drawing on (mostly untranslated) writings by Ukhtomsky and his students, particularly Nikolai V. Golikov (1905–1988) and Vladimir S. Rusinov (1903–1995), it is reviewed how in this tradition, the combined effects were analyzed of graded (and electrotonic) potentials, spike-structured neural activity and specific transmitter systems. This is particularly interesting, as the potentially profound organizing effects of graded potentials and field effects on specific synaptic transmission have long remained controversial, but in recent years, are strongly reconfirmed by new findings – seen as opening a new chapter in their study (Fröhlich and McCormick 2010; Mann and Paulsen 2010). Examining such effects as part of the dominant mechanism for rapid forms of neural homeostasis and excitability modulation may present particular interest for future studies. Furthermore, considering related lines of modern research, it's interesting to note that according to their authors, it's "shocking" how late the whole field of neuronal homeostasis emerged in the West (Marder and Tang 2010). Indeed, this has occurred only in the last few decades, which is striking given the reliance of essentially all organismic and physiological processes on homeostatic phenomena, and their key role in the integrated study of organisms. In this context, determining the reasons for this respective delay may be interesting, as well as exploring the further implications of the dominant framework for current research. To our knowledge, this chapter is the first and the only one so far to review this general problematic in its modern and historical contexts. As such, it provides starting points and outlines for further work in this direction, rather than a conclusive argument or more detailed elaboration (which would call for collaboration with specialists in respective fields). On the other hand, the advances occurring in the last years make such reassessments perhaps more possible and timely than ever, given the increasing convergence of historical and modern ideas documented in this paper.[4]

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[4] In this regard, the recent works on hormetic phenomena in neuroscience may be of particular interest (Calabrese 2008; Mattson 2008), and further demonstrate parallels between current and historical research (of which the author became aware of only after writing this chapter). Hormetic phenomena reflect the state- and dose-specific variations of cellular reactions to the same stimuli under different conditions, and highlight the ordered nature of these response changes over time. This leads to problems of reaction variability and dynamic

At the same time, other aspects of the conceptual approach and problematic of Ukhtomsky's dominant remain more difficult to analyze from current perspectives. This concerns specifically the way multiple questions, now addressed in the broad rubric of complex systems research in biology, were integrated into the basic fabric of the dominant concept, and given qualitative and physiological formulations before respective modern ideas and areas were introduced in the exact sciences. Furthermore, it concerns the ways the dominant concept spans between these and psychophysiological problems and domains, as discussed in the next chapters.

In chapters two and three, by drawing on direct collaborations with the physiologist Lucia P. Pavlova from St. Petersburg State University, and her decades-long work in human labor and psychophysiology (Pavlova and Romanenko 1988), it is shown how ideas of the dominant have anticipated in detail current findings, and lead to important findings in the field of human neuroscience. These are shown to remain relevant both in methodological and empirical terms, and specifically, for approaching human neurophysiological events as complex time-variable processes in naturalistic settings.

In chapter two, it is shown how the problem of chronogenic, systemic-dynamic organization of cognitive functions remains one of the most difficult and challenging tasks for modern cognitive science and neuropsychology. Analyzing this presumes that the localization or mapping of cognitive processes to neural systems undergoes systematic and significant shifts not only during ontogenetic development, but also during the "microgenetic" developments related to skill acquisition, practice, and related forms of human activity occurring on the rapid time-scales of behavioral change and modification (i.e., learning, plasticity). As very few studies have so far specifically addressed this problem, the historical sources and contributions of Russian schools may prove to be most relevant and current in this regard, particularly as it's there that they were first and most specifically formulated. This is shown with respect to the psychological traditions of Lev S. Vygotsky's (1896–1934) school, their connections to Ukhtomsky's dominant, and the modern research directions related to chronogenic localization.

These materials are particularly interesting, as it's currently argued that neuroscientific and EEG approaches have never been applied to the problems of human cognitive control levels and dynamics, such as operator work and its cognitive control analysis in real time (e.g., to determine whether a human operator is performing a task as an automated routine at *skill* level, as procedures-based activity at *rule* level, or as a problem-solving process at *knowledge* level) (Borghini et al 2017). This problem, apparently true for modern traditions, is all the more significant as it's an area that is exceptionally important not only theoretically, for the development of ecologically valid and integrative psychophysiology, but also for human safety and risk management, particularly in conditions involving high psychophysiological work-loads in time-constrained environments (such as encountered in many vital professions, e.g., rescue operations, air traffic control, etc.). At the same time, related research traditions in the USSR go back into 1960-s, and through the application of

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excitability change similar to those investigated in the Ukhtomsky-Wedensky school (and summarized in ch. 1). Indeed, the parallels have been recently explored between modern hormetic research and the tradition of D.N. Nasonov (Agutter 2007; Matveev 2005), who's school of cytophysiology followed closely in the tracks of the Wedensky-Ukhtomsky tradition. What is significant, however, is the fact that modern hormetic research, remaining confined almost exclusively to the field of toxicology, has been seen as a "problem in the wrong discipline", as well as a model in search of a general theory (Stebbing 2003). In this context, it seems appropriate to ask whether the research traditions in the dominant paradigm (extending over a hundred years) may not contribute to such a general theory or framework – needed to recognize the role of hormetic phenomena beyond toxicology, in the neural homeostasis of physiological and behavioral conditions (as its proponents call for) (Mattson 2008; Calabrese 2008).

dynamic EEG analysis, have led to numerous important results in the dominant framework. This includes the demonstration of the stage-wise elaboration of cortical work dominants, the coupled inversion of brain activation gradients within and across hemispheres, and their distinct dynamics in particular task settings (Pavlova and Romanenko 1988). All of these testify to the importance of distinguishing external behavioral manifestations from their underlying neurophysiological mechanisms, often highly variable also within individuals, both in the micro- and macrostructure of activity. Furthremore, the diagnostic value of the dominant framework for determining intra- and interindividual cortical functional states – including their adaptive and non-adaptive features (Pavlova 2015, 2017), has important implications for functional state correction and therapeutic intervention in healthy and clinical populations.

In the same chapter, it's further underscored that the key concepts and frameworks informing related modern studies – specifically the theories of dual processes of mind and cognition, appear to overlap extensively with the notions of higher (culturally mediated) and lower, biopsychological processes, as introduced by the psychologist Lev S. Vygotsky already in the 1920-s, and further elaborated by his students Aleksandr R. Luria (1902–1977) and Aleksei N. Leontiev (1903–1979). Although these belong to some of the longest and most significant psychological research traditions in the 20-th century, and continue well into the present time, their relevance for dual-process theories has apparently not been so far discussed. While this paper remains restricted to the works and ideas related to the dominant, further examination of this theoretical convergence would be a highly interesting and desirable task for related fields, given their widely shared concerns and features.

In chapter three, the methodological and technical specificity of this line of dominant studies is further highlighted and applied to a different case study in human neuroscience – the analysis of cerebral and psychophysiological functional states during university oral exams in subjects with various degrees of success in the task. Similarly like the previous chapter, this co-authored paper draws on previously published results and findings (Pavlova and Romanenko 1988), with the aim of placing them in new theoretical perspectives and relating them to modern Western approaches. Specifically, the interconnections of the dominant approach and the opponent process framework of R. S. Solomon and colleagues (Solomon and Corbit 1974; Solomon 1991) are explored as a framework for analyzing homeostatic and cognitive changes in realistic conditions, involving EEG analysis of university students in real time exam settings. The reported findings most likely generalize to many other stressful and high-performance tasks.

In the opponent process theory, the homeostatic regulation of motivational and affective states has been specifically examined, and found to be subject to regulatory changes that may involve over-compensatory effects in the direction opposite from the initially experienced state (at least in particular conditions or states). This theory has been particularly influential in clinics and the analysis of addictive and pathological dynamics, although its relevance for normal physiology and stress physiology has been also recognized, and awaits further study (Ekkekakis et al 2005).

In this paper, these aspects are for the first time explored from the perspective of the dominant, and related to the "super-compensatory" effects that have been observed earlier in dominant processes and labor psychophysiology (Pavlova 2017). This points out that the opponent dynamics analyzed by Solomon and others may represent special instances of a more general class of self-regulatory physiological phenomena; in these cases, before restoring the set-point level of a deviated physiological parameter, its value overreaches in the opposite direction, and thus disturbs the initial homeostatic equilibrium even further before restoring its original baseline. Such phenomena may be particularly significant for stress and exercise physiology, as well as developmental biology, where compensatory reactions with energetic over-shoot or "surplus anabolism" have been documented

(Arshavsky 1982); however, it seems that little is known about the difference between normal and pathological super-compensatory processes, their different subtypes, and relevance for general brain dynamics, particularly in natural settings of human activity (Schulkin 2004; Pavlova 2017). In this context, the materials presented in the paper should be highly interesting, by showing how in a naturalistic setting, the registered fronto-occipital and inter-hemispheric activation gradients both appear to display "over-compensatory" (or opponent-type) self-regulation in healthy human subjects, apparently as a part of normal physiological homeostasis in stressful conditions.

In this chapter, the methods and principles are covered in more detail that allowed to apply the dominant framework of EEG analysis to these ecologically realistic, and technically challenging experimental conditions. Indeed, the included literature review indicates that in the intervening decades, no further attempts have been made by other research groups to record human EEG activity in similar settings, engaging subjects in immediate social interactions and verbal communication in final exam context. This points to important aspects of the dominant framework, the methods and concepts of which have been specifically designed to address complex dynamic settings.

Specifically, on the basis of works in the Ukhtomsky-Wedensky tradition, and in collaboration with specialists in the mathematical analysis of complex time-varying signals (non-stationary stochastic processes) (Sergeev et al 1968), methods and techniques of EEG analysis were designed that are specifically sensitive to the individually and temporally variable nature of physiological and psychophysiological processes – including rapid, qualitative shifts in human functional states. This is frequently observed in natural conditions of human brain activity, both at rest and at work (Pavlova and Romanenko 1988). While technically related approaches have been later developed also by other groups (Fingelkurts and Fingelkurts 2010), in terms of its applicability to the environments of human performance and work, the dominant paradigm appears to remain most specific for assessing rapid functional state changes in the human brain, and their intra- and interpersonal variability in dynamic conditions. The current references included in the above chapters (2 and 3) testify to this conclusion, and support further studies in the dominant framework of human neuroscience, both on methodological and empirical grounds.

In light of the above studies, it appears that one of the most likely historical reasons for such notable divergences in human neuro- and psychophysiological research traditions in the West and the USSR may be related not only to the school of the dominant per se, but to the associated wider perception of labor physiology and psychology as branches of fundamental and theoretical science (rather than solely applied disciplines). It's highly probable that due to such historical and social reasons, studies in human labor and performance never attained a comparable status as paradigms for basic research in the West. This may have important implications for the way neuroscientific studies are designed and evaluated, however – including their ecological aspects, in particular.

That Ukhtomsky is considered the founder of theoretical labor physiology in the USSR (Zolina and Izmerov 1983) was underscored in this context. The conceptual and theoretical aspects of the dominant research, addressed below, may also be understood in this light.

3. Theoretical aspects and future outlooks

The observed scientific parallels and divergences may perhaps not surprise historians of science, or life and cognitive scientists well aware of the methodological diversity and historical complexity of their disciplines. Specifically, the neurobiologist S. Rose has repeatedly commented on this unusual historical of methodological development in the neurosciences: "... the non-reductionist approach to neuroscience and psychology guided research during the earlier years of the Soviet period in Russia

with conspicuous success, in the hands of such figures as Vygotsky, Luria and Anokhin. […] As I've pointed out previously, modern neuroscience – and most specifically Anglo-Saxon pragmatic reductionism – ignores these earlier insights to its disadvantage" (Rose 2005: 62, 189-190). This restates claims from his prior work, observing that "As, at least in neuroscience, the theoretical limitations of naive reductionism become increasingly apparent, and cold war suspicions recede into history, the time is ripe for a re-assimilation of the autonomous Soviet tradition in neurophysiology and psychology into a more integrated and universalistic neuroscience" (Rose 2012: 269-270). Nonetheless, it's observed that on the whole, the mentioned theories have not been well received by Western science, and in more recent decades, following the adoption of Anglo-American methodologies in the former USSR, these potentially fertile traditions have been largely obliterated also in their homeland (Rose 2005). In this context, the question is not only how certain research programs were able to produce works that were significantly ahead of their time, but how and why their reception has been or continues to be hindered by socio-cultural, political, or other extra-scientific circumstances. This phenomenon is of course by no means exceptional or exclusive for the traditions of USSR research, but relevant for many other ones not discussed here (e.g., Danzer 2011). Addressing such problems goes beyond the scope of this thesis, and has been discussed elsewhere (Klempe and Smith 2016). Such considerations may help to explain the fate of research programs independently from their scientific merit.

It may be expected that among sciences, the life sciences are particularly affected by such difficulties considering the complexity of their research subjects, and the diversity of different approaches, theories, and scientific schools this complexity is likely to encourage. The Kuhnian conceptions of the historical succession and exchange of different scientific paradigms notwithstanding, it's true that even in a science as objective and rigorous as physics, instead of a historical succession, multiple research paradigms have long co-existed (as no theoretical unification has been achieved between classical, quantum, and relativity theories). Nonetheless, in an area as inherently diverse and historical as biology, it may be more appropriate to ask whether larger theoretical unification and synthesis is in principle achievable, at least on similarly formal and rigorous grounds. Indeed, in contrast to the universal laws studied by the physico-chemical sciences and paradigms, the life sciences must inevitably deal with the historically and individually variable, contingent products of evolution (Kauffman 2014; Markoš and Švorcova 2019; Mayr 1982). Being subject to exceptions and violations, the rules and regularities of life possess a qualitatively different ontological and scientific status, and can be seen as markedly distinct from the universality and homogeneity of lifeless phenomena and laws with "nomothetic", inviolable and universal properties (Elsasser 1987).

Indeed, the question of historicity was central to many traditions of Soviet research – where not only biology, but even neurophysiology was recognized as a highly autonomous field of science, with its own distinct methodology and philosophical problems (Mecacci 1979; Graham 1987). This historical view, although still exceptional in neuroscience (relying heavily on ahistorical, technical disciplines), may prove crucial for any integration of its subject matter and problems into more systemic frameworks. This integration must not, and probably cannot in principle, successfully imitate the methods of physics and nomothetic sciences (Elsasser 1987; Rosen 2000); instead, recognizing the problems of historicity and emergence as fundamental for life and neurophysiology may be central in this regard.

Ukhtomsky in particular stressed consistently the deep implications of evolutionary theory and thinking not only for theoretical biology, but also for physiology – a discipline frequently seen, even nowadays, as restricted to the "proximate" causes and mechanistic aspects of functions, clearly distinct from their evolutionary and historical dimensions (Mayr 1982). In a marked contrast to this

dichotomic view, the dominant framework underscored as its central motive that also in the micro-intervals of time, the workings of bodily organs and systems are highly variable and may show complex temporal interferences, the analysis of which should be founded on the notions of irreversible and non-linear dynamics (Ukhtomsky 1978), instead of simpler mechanistic and ahistorical concepts. Such requirements and challenges remain entirely actual (Anderson et al 2012; Cohen 2011; Dotov 2014), and become acute as the attention of investigation turns from isolated, artificially constrained and reduced physiological systems to the study of their normal eco-physiological functioning – such as prolonged or heightened work-loads, frequently observed in human labor and cognition (ch. 2 and 3). In such cases, it's particularly clear how the same physiological unit may begin to exhibit qualitatively different patterns of function, and behave as a "new system" with distinct global properties over work course. From a theoretical and philosophical perspective, Ukhtomsky highlighted the difficulties such conceptions present for classical ideals of scientific practice, and its methods of isolation and abstraction in particular, including abstraction from time:

> The dominant principle, as well as some other positions of the school of N.E. Wedensky, present certain difficulties and unexpectancies particularly to those physiologists who are accustomed to characterizing the organs and mechanisms of the body by constant formulas, independently of time and separately from one another: a certain nerve is always inhibitory for a certain organ; a certain hormone always lowers basal metabolism, etc. It's a completely natural situation in science when it studies isolated organs in the laboratory, and in these conditions determines their most consistent statistical features – as this was done in the so-called "special physiology of organs". In reality, it would be more correct and accurate to say that in precisely defined conditions and particular time intervals, the organ functions as it's supposed to, according to a constant rule, and in line with experiments of its isolation and isolated stimulation.

> No mean amount of misunderstanding and contradictions arise in science only because we haste to take as general and independent of time those characters that were obtained in particular circumstances. We are, of course, correct in concluding that the living organism is characterized by unitary activity. It would not merit to be recognized as an organized whole if it weren't capable of at least relative unity of activity. But we are also correct in saying that the organism is a multitude of diverse organs and mechanisms, each with its particular function. Both features of organisms, when extracted from reality, appear thereafter as irreconcilable contradictions that are hard come to any terms with. It's assumed that to keep one of them, the other needs to be sacrificed. Instead, such contradictions arise only because we're accustomed to taking each characteristic outside time, and then also force them to meet one-another outside time. The contradictions disappear, and in their place appears a living and most interesting reality as soon as we notice that the organism in its factual flow represents a multitude of diverse events, which from time to time are able to assemble into nearly or fully-connected mechanisms, for the first time making it possible for the organism to attain a particular result in its natural environment. (Ukhtomsky 1966: 149)

To highlight but one example of the implications of this shift of perspective for modern science, the recent proposals of dual coding theory may be considered (Daniels et al 2017). These have shown by a new, two-phase model of neural decision-making that the decades long opposition between network-based and single-neuron models of information encoding may be possibly resolved by taking a temporal-dynamic approach to the problem, recognizing that the extent to which information is distributed in a network, or encoded in the firing of particular neurons changes as a function of time and decision-making (Daniels et al 2017). This may be seen a novel approach to some of the largest and still open debates in neuroscience, the traditional formulations of which in atemporal terms may have long precluded its logical resolution and formulation. Not incidentally, a related temporal-dynamic approach to decision-making was long ago formulated by Anokhin (1974, 1984; cf. Tsitolovsky 2015), in proposing that the inter-relations of brain functions (and single cell behaviors) undergo

qualitative changes in the course of a behavioral act, and the decision-making state in particular (Tsitolovsky 2015). Indeed, this view follows closely from Ukhtomsky's own formulations on biological time, as considered in ch. 1. (cf. pp. 32). More generally, the traditional neglect of such process-dynamic and developmental aspects from neuroscientific explanations and paradigms raises important theoretical questions, and is most likely relevant to explaining also the observed discrepancy of neural homeostatic research in the West and the Russian/USSR traditions (including the problem of hormesis, cf. footnote 4, pp. 6-7).

The above positions, outlining the critical views of Ukhtomsky's school, indicate at the same time its alternative strategy towards scientific explanation and experimentation. These are driven towards the elucidation of *dynamic regularities* that underlie, or emerge in the course of physiological processes as time-variable events. From such events, particular mechanisms and statics arise only as secondary and transient products (e.g., of reiterative decision-making). This fact necessarily shifts the focus of key explanatory significance and integration from the mechanistic level to the one above it – the level of organizational processes, as proposed for heuristic purposes (Fig 1).
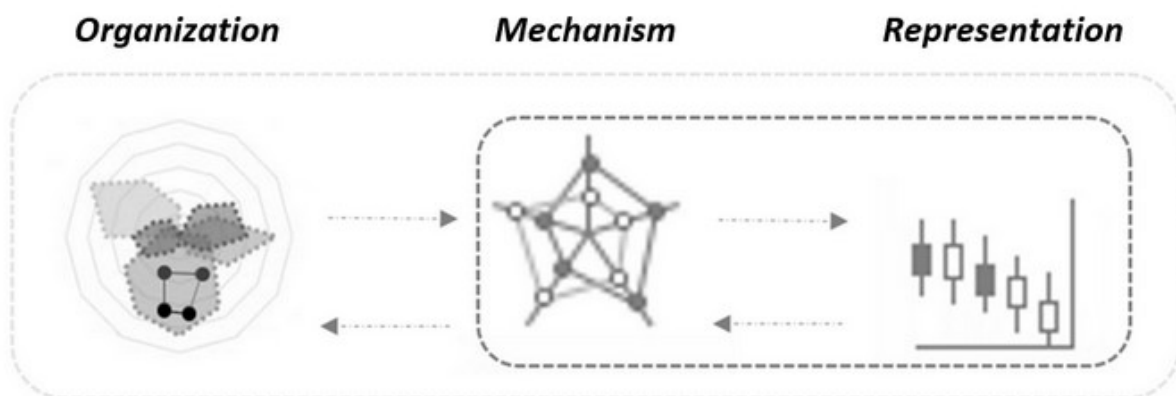

Fig 1. Schematic depiction of levels of modelling. The figure depicts an explanatory process or hierarchy, involving transitions between the 1) systems-level organizational processes and relations, identifiable at the concrete organismic level; 2) their causal analysis in terms of particular component mechanisms, their material and efficient interactions; and 3) the descriptive analysis of such mechanisms in representational terms (such as statistical and correlational analysis). These levels can be distinguished for heuristic and analytical purposes, and may normally be thought to closely inform and constrain one-another both explicitly, according to a prevailing theory, or implicitly through assumptions guiding scientific practice in the field (neuroscience).

In current terms, the particular causal processes and manipulations involved in the mechanistic level are likely to remain ambiguous, or insufficient unless their effects are interpreted in the framework of sufficiently specific (and robust) organizational constructs, such as the dominant. At the same time, considering the time-varying and complex properties the latter may exhibit, not only is variability implied in the mechanisms that instantiate it in particular cases, but also the representational tools used to analyze these mechanisms must be appropriately chosen – i.e., to deal with non-stationary time series, and avoiding statistical techniques that average over longer time epochs or across wide frequency bands of the EEG (Sergeev et al 1968; Pavlova and Romanenko 1988; Fingelkurts and Fingelkurts 2010). Such aspects, although not addressed here in technical detail, may illustrate well the generally close inter-dependencies existing between the various levels of analysis and modelling in neuroscience, and the frequent transfer of concepts and ideas from one level to the other (often implicitly or unconsciously) (cf. Labra-Spröhnle 2017) (Fig 1).

It was noted above that although in the West, significant traditions of theoretical biology exist with a focus on the organizational principles of life, such as its dynamic self-assembly and anticipatory organization (Rosen 2012; Maturana and Varela 1987, 1991; Hofmeyr 2017), these problems have found surprisingly little attention in the neurosciences (Anderson et al 2012; Dotov 2014). Indeed, the wide variety of basic and more applied fields comprising it appear so far mainly concerned with mechanistic and representational lines of analysis – to an almost complete exclusion of organizational and organismic problematics from the field's theoretical foundations (e.g., to incorporate evolutionary, developmental, and behavioral physiological analyses) (Krakauer et al 2017; Frégnac 2017). Accordingly, in the field of theoretical neuroscience, it appears that no concept exists of modeling the organism as an evolutionarily and developmentally integrated whole, and attempts to model its brain activity in abstract terms are carried out almost solely on representational levels, using quantitative principles drawn directly from other, non-biological and non-historical fields (Abbott 2008; Barandiaran and Moreno 2008; Bickhard 2015a). While this has no doubt led to major technological advances, and allowed unparalleled sophistication and insight in certain aspects of quantitative modeling, its relevance for advancing causal mechanistic analyses remains largely open – as pointed out particularly in relation to various neural network models at the center of this discipline (Rubinov 2015; Bickhard 2015b). Indeed, it is observed that even the more physiologically and mechanistically oriented lines of modern brain research – involving direct experimental interventions, to test the causal conditions of particular neural processes – proceed almost without any reference to organism-level phenomena, such as behavior, development, and evolution (Krakauer 2017; Bateson 2009). Thus, similarly to the descriptive level, also mechanistic analysis has in modern research largely evolved as an autonomous area with its own concerns and agenda – the problems of which rarely intersect with those of behavioral biologists, organismic and comparative physiologists, or evolutionists, among others.

It is on this background that the early traditions discussed in this thesis should present particular interest, showing prospects for theoretical developments in the field. To illustrate this, we highlight a list of problems and organizational phenomena that were formulated by Ukhtomsky and colleagues. These were mostly presented in qualitative and physiological terms, but increasingly over time, with a view on their possible future formalization based on new branches of complex systems analysis, such as the theory of non-linear oscillatory systems (Ukhtomsky 1978: 187-194). In this respect, Ukhtomsky and colleagues took the first steps towards laying out this problem in more formal terms, and offering what is probably the first application of this theory in neurophysiology (Zueva and Efimov 2008, 2010). Complementing the concept of the dominant as an object of physiological investigation, such modelling principles present some of the tools needed for their appropriately complex organismic analysis. It can be noted, however, that most of these problems remain little addressed to this day (Zueva and Zuev 2015).

1. The problem of non-linear oscillations. This aspect has been commented on by several later authors and more technical studies (Gulyaev 1967; Ohnyanskaya et al 1990; Zueva and Efimov 2008, 2010), and is particularly important for understanding a key problem of the teaching. This lies in determining under what conditions and how a particular nerve center may obtain dominant properties, with the associated ability to entrain, coordinate, or suppress the excitation rhythms of other ensembles. These aspects would be crucial for overcoming the "mechanical schematism" (Ukhtomsky 1978: 187-194) of the still widely prevailing views, according to which the most highly active and excited brain center is necessarily also the dominant one – a notion that contradicts observation, and would trivialize the problem of dominance as a largely tautological notion (i.e., post factum, the prevailing reflex and neural system can always be declared "the stronger" and dominant one) (Ukhtomsky 1978). Instead, the precise demonstrations that even very weak signals, if properly timed and positioned, may evoke

significant non-linear effects on complex systems is seen as a key problem for the dominant (Ukhtomsky 1978: 187-194). In his first paper on the dominant principle, Ukhtomsky had succinctly summarized what he saw as the main result implicit in his mentor Wedensky's teaching: that the performance of an organ is a function of its ongoing physiological state (Ukhtomsky 1966: 5). As he later recognized, this was a simple periphrasis of the fact it's a non-linear oscillatory system (Ukhtomsky 1978: 194). This comment refers to the fact that in Wedensky's school, functional state changes were analyzed in terms of differential reaction inertia – recognizing not only that different links or subsystems of an organ (e.g., the brain, or neuromuscular apparatus) may possess different inertial properties, but also the fact that in the course of its own functioning, these inertial properties are likely to change and diverge in an ongoing and heterogeneous (heterochronic) manner in the observed tissue. This highlights the complexities of its formal analyses, and indeed, the necessity of understanding the observed systems' physiology in good detail before attempting its formalized and quantitative modelling. However, with regard to the theory of non-linear oscillations, it's observed that even now, its formal models have remained insufficiently studied to allow comparisons with the results of physiological experimentation (Zueva and Zuev 2015). The co-authored papers presented in this theses have in their technical aspects and background proceeded from different formal bases, following from the theory of non-stationary stochastic processes (Sergeev et al 1968). However, the criteria for its physiological interpretation proceeded from the precise problems and physiological analyses of dominants as complex, time-variable systems constrained by human activity (Sergeev et al 1968; Pavlova and Romanenko 1988).

2. The problem of stochastic facilitation. Since the 1980-s, when the phenomenon of stochastic resonance was first defined in physics, a broad range of biological studies have investigated the possible benefits of noise for signal detection and information handling in living systems, and the nervous system in particular (McDonnell and Ward 2011; Moss et al 2004). In statistical physics, the phenomenon has a precise definition, and under the term "stochastic resonance" refers to the situation where the presence of a weak periodic input to a non-linear dynamical system can be detected from its responses only in the presence of noise added to the system (McDonnell and Ward 2011). In biology, the broader term stochastic facilitation has been proposed, to include a larger variety of biologically relevant phenomena and mechanisms where qualitatively similar benefits of noise have been observed – including not only for signal detection, but also for various functional benefits in system performance and optimization, including rehabilitation (McDonnell and Abbott 2009; McDonnell and Ward 2011). In the current context, it's interesting to underscore that this aspect of the dominant appears so far not analyzed or highlighted. By specifically investigating the preconditions for dominant reactions and their facilitation by extraneous stimuli and competitive reactions (i.e., "noise"), it may nonetheless seem that the dominant paradigm was perhaps the first to describe and analyze in detail related forms of facilitative phenomena in the nervous system. Indeed, the large variety of models where dominant reaction reinforcement by unrelated stimuli were described (Ukhtomsky 1950–1962; Airapetyants et al 1967; Batuev et al 1990) may yet prove of interest for future research. It's currently observed that due to the narrow focus of most related studies, and the tradition of modelling them by physical definitions and criteria (e.g., for signal detection), its biological aspects and conditions have remained little examined, and have mostly been defined in overly restrictive ways. Interestingly, some of the most important but unresolved scientific questions about stochastic facilitation are currently those that concern "whether, or when, biologically relevant noise is exploited to benefit neural systems, and if so, precisely how this occurs" (McDonnell and Ward 2011). By virtue of its well-described physiological and synergetic properties (Zueva and Efimov 2010), the dominant appears to be a phenomenon of significant interest in this regard, and may potentially help overcome some of the mentioned difficulties in this field. This includes specifically the "systemic failure" to

consider the biological appropriateness and broader definitions of stochastic resonance (McDonnell and Ward 2011), and the need for new experimental setups and theoretical approaches, with a focus on biological realism.

3. The problems of biological non-equilibrium and work. Although during Ukhtomsky's lifetime, the cellular and bioenergetic mechanisms remained unknown that could lead to increased functional capacity and energetic gradients in the course of physiological work, it's important to note how closely these aspects were anticipated by him at the physiological and organismic levels. In a recent review, Igamberdiev (2012) has credited I. Arshavsky with first introducing the idea of "hyper-restoration" into the field of muscle physiology (Arshavsky 1972), with his demonstration that as a result of its motility, the energy spent by muscles is later restored at a surplus level, and this "surplus anabolism" supports the growth and development of organisms (Arshavsky 1972, 1982; Igamberdiev 2012). On the other hand, as his student and follower, Arshavsky particularly credits Ukhtomsky with first formulating the problem of activity as a general biological problem for physiology (Arshavsky 1990), including neurophysiology in particular. To this day, relevant aspects on brain function appear little explored and systematized, and Ukhtomsky's principled turn from a reactive and physicalistic view of external stimuli to an active, chemical-catalytic view of their effects remains interesting for neuroscience, and for human neurophysiology in particular. This problematic rose to the fore starting in late 1920-s, with studies on the *assimilation of rhythms* by himself and colleagues (Golikov N.V., Vasilijev L.L.) (Ukhtomsky 1978). This line of experimentation gave rise to new views of stimuli as potential catalytic agents, acting to increase or decrease the rate of autochthonous chemical cycles in tissues. In this context, the assimilation of rhythms is indeed a general biological problem, reflected in the adaptation of the autochthonous pace of tissue reactions and chemical cycles according to ongoing activities, including the rate and rhythms of nervous discharge and the events evoking them. This type of organismic autocatalytic events were seen as laying at the basis of training, many forms of learning, physical exercise and labor activities in humans particularly (Merkulov 1960). Their interesting aspect lies in the fact that besides spending energy, such processes can increase the levels and rates of metabolism, and lead to new reaction norms and increasingly strong dominants – i.e. subthreshold, stable and persistent "stationary excitation systems" in the brain. Related problems of work capacity remain particularly interesting also from evolutionary and anthropological perspectives, considering that according to recent genomic findings, some of the major innovations in the human lineage are associated with genomic changes in the control of energy metabolism in the brain (cf. Prochiantz 2010), and that significant, disproportionate differences are found in the metabolic rate of humans and our closest primate relatives (including in basal metabolic rate) (Pontzer et al 2016). At the same time, the implications of these bioenergetic questions for theoretical neuroscience and human psychophysiology appear little considered, particularly with respect to the effects of the possible inter- and intra-individual variability of related bioenergetic measures, including their possible plasticity and modification. Addressing related questions will likely depend on advances in epigenetics and integrative neuroscience.

4. The problem of critical stability. This refers to new lines of modelling that analyze the brain as a system that is balanced at criticality – a meta-stable condition associated with numerous optimality criteria, and related to the delicate and dynamic balance of inhibitory and excitatory neurotransmission. It is currently a major challenge to understand the precise biological and physical mechanisms through which the brain arrives at and maintains criticality (Shew and Plenz 2013), and by these means, retains optimal responsiveness and stability to various inputs in highly dynamic conditions. Interestingly, this problem seems to have a close parallel in the way Ukhtomsky interpreted dominants as non-equilibrium formations close to a phase transition (Kryukov 2005). Indeed, the analogy of physiological changes to transitions in the aggregate states of matter was drawn already in

his first paper on the dominant in 1923 (Ukhtomsky 1966), the first passage of which highlights the new prospects opening for physiology by the recognition that similarly to physical systems, also the functional condition of physiological systems may go through qualitative transitions, such as shifts between inhibitory to excitatory dynamics in the same region, under changing conditions. The dominant is a particular manifestation of such variability and transitions inherent in nervous tissue – whereby its particular subregions may support a large variety of constellations and functions, depending on the location of the dominant focus. There are several aspects of this teaching that remain of particular interest in this context, including the notion of the stage-wise formation of dominants, including its passage from weakly stable and non-concentrated forms, where the effects of collateral inhibition are setting in, to its more concentrated expressions, with pronounced reinforcement from unrelated stimuli – and finally, to the dominant's (auto)inhibition, either gradually or through a rapid transition (Ukhtomsky 1966). This type of chronogenic and historical regularities (no doubt, possible to break down into more precise phases, cf. Gulyaev 1967), occurring in particular conditions of work and in particular organisms, may yet prove fundamental, if the physically inspired complex models of critical balance and stochastic facilitation are applied to in vivo neural systems, including the dynamical functioning of the human brain in its natural environments. This appears particularly relevant, as until recent years, predictions of formal criticality parameters have remained untested in real living brain tissue in Western research. Specifically, as observed in ch. 1, "experiments on the in vivo homeostasis have not yet been performed with attention to the possibility that criticality may be the end goal of homeostatic processes" (Shew and Plenz 2013), and the implications of this conditions for normal and abnormal cortical function have only begun to be explored.

<p style="text-align:center">*   *   *</p>

We have offered this list of areas above since to our knowledge, they have so far not been brought together to highlight the extent to which the dominant paradigm has not only anticipated modern research, but continues to pose precise questions and challenges for future research. Naturally, addressing them belongs to the technical specialists in relevant fields of biological complexity; however, formulating these problems as chronogenic in nature and highlighting their biological and physiological aspects is a task that appears in many cases necessary not only for historical reasons (e.g., to understand the methodology of the dominant), but also for the lack of comparable modern research programs, investigating the above problems from integrated theoretical viewpoints. On the other hand, this would most certainly be worthwhile and necessary. Indeed, it's currently noted that the "search for a unified theory […] remains at a rudimentary stage for the brain sciences" (Frégnac 2017) – and while ever increasing amounts of data are generated, due to a lack of parallel efforts in basic theory, "all sense of global understanding is currently in acute danger of getting washed away" (Frégnac 2017). In this context, the early historical research paradigms investigating problems of neurophysiological organization and qualitative biological complexity may appear to remain still some of the most fundamental and valuable contributions to theoretical neuroscience as a biological and naturalistic discipline, on the basis of which a historically oriented paradigm of human neuroscience could also be built.

The above complex areas were also highlighted since to our knowledge, they have not been referred to together in addressing the dominant paradigm, yet they help to articulate some of its distinct aspects and emphases both in comparison to modern research, as well as to historically closely related research programs. A particular further aspect to consider in this regard is the question of model-based anticipation and self-regulation, which came to occupy a central ground in the works of Bernstein and Anokhin, but not in Ukhtomsky's own research (at least not explicitly). Although this is partly a matter

of terminology and designation, it's one of the reasons why the ideas of model-based anticipatory processes (Nadin 2015; Rosen 2012) remain more difficult to relate to Ukhtomsky's works than to those of his successors, directly involved in the establishment of biocybernetics in the USSR (Bernstein 1966; Anokhin 1974). Partly for this reason, instead of the designator of "anticipatory physiology", the more general designator of "organismic physiology" has been adopted in the title of this thesis. This qualifies Ukhtomsky's approach and its holistic orientation, without necessarily making more explicit commitments to its interpretation from particular Western traditions, either modern or historical (e.g., including that of "organicism" – another closely related intellectual current in holistic biology: cf., Allen 2005; Nicholson and Gawne 2015). This refers both to its focus on the organizational level of processes in the nervous system, as referred to above (Fig 1.), as well as the recognized need to consider its functions from the perspective of the organism in its historical development – in evolutionary, ontogenetic, and physiological time-scales (Perlman 2000; Burggren and Warburton 2005; Arminjon 2016).

The above-mentioned problem areas may also highlight avenues for new approaches to "anthropological physiology" (von Weizsäcker 1968; Buytendijk 1974; Fagot-Largeault 2009), by contributing towards new tools, methods, and approaches in human neuroscience (cf. Labra-Spröhnle 2016). Indeed, this seems to be the main requirement for related early ideas to be developed further (Dekkers 1995), which regardless of their theoretical interest and significance appear to have made little empirical impact on experimental or clinical research (Wiggins and Schwartz 2013). The physiological concepts and methods addressed in this thesis may in this regard represent particular interest, and complement the more philosophical, phenomenological, and speculative ideas that have been developed in earlier literature on related problems. These include the unity of the organism and its environment, their interrelations in organism-centered and historical terms (not only descriptive informational or physico-chemical ones), and the variable meaning of external events and signals in different contexts, particularly for human subjects (von Weizsäcker 1968; Buytendijk 1974).

With few exceptions, however, such holistic ideas remained still fragmentary in their physiological foundations, and were often limited by indirect support – e.g., from studies proceeding from various methodical and methodological background, by other authors (Buytendijk 1974; Dekker 1995). Of course, the same may be said about current attempts to relate the dominant concept to modern science – such endeavors are bound to highlight important differences in method or theory for any particular parallel that is explored. Furthermore, since the 1990-s, the number of direct experimental and original empirical studies on the dominant has been in rapid decline, and to our knowledge, no new paradigms for its complex study have been developed in recent years. Even at its home university in St. Petersburg, the formal institution having long supported related work and legacy has been recently closed, as the A.A. Ukhtomsky Institute of Physiology was disbanded in 2007, and its place taken by standard research programs in neuroscience and physiology.[5] This result, marking the end of long processes of scientific change in recent Russia, reflects both officially and symbolically the end of support for related lines of complex physiological study, and the perception of the latter as belonging to history even in their homeland. This circumstance, combined with the wide adoption of more reductive, Anglo-American perspectives mentioned above (Rose 2005) may also indicate the wider difficulties faced by fundamental and theory-driven research in the current era – increasingly dominated by extreme specialization, data-driven research programs, and minimal interest for holistic theory construction (Frégnac 2017). At the same time, the large-scale brain modelling and

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[5] The official statement can be found here: http://guestbook.spbu.ru/prorektory-spbgu/tunik-sergej-pavlovich/1037-o-nauchno-issledovatelskom-institute-fiziologii-im-akademika-a-a-ukhtomskogo.html. [Retrieved 10.07.2019]

industrialized imaging projects underway proceed on largely ahistorical grounds, with little or no guidance from fundamental theory, including evolutionary and developmental concepts (Bateson 2009). As such, their relevance for neuroscience as an ecological and complex discipline will remain inherently unclear.

Therefore, without addressing related historical and organizing concepts in its basic paradigm and agenda, it may be asked whether the wealth of data and findings coming from more reductive modelling strategies in brain research will ever be able to contribute to "a more integrated and universalistic neuroscience", as desired (Rose 2012: 269-270; 2005). For the latter, the problems of history and its organizational modelling will likely need to be readdressed and considered anew in many respects. It is hoped the studies included in this thesis encourage further work in this direction.

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2. PUBLISHED STUDIES

STUDY 1.

Kurismaa, A. (2015). Perspectives on Time and Anticipation in the Theory of Dominance. In: Nadin, M. (Ed.), *Anticipation: Learning from the Past* (pp. 37-57). Springer: Cham.

Author contribution:
Original study, conceived and drafted by the author.

Perspectives on Time and Anticipation in the Theory of Dominance

Andres Kurismaa

Abstract. This paper introduces the problem of anticipation in the theory of dominance by A.A. Ukhtomsky and his school of neurophysiology in the light of recent research. The works of this school represent an original integrative approach to functional state dynamics in the brain, both in its general biological principles and physiological mechanisms. It is proposed that this approach may help to ground novel frameworks and hypothesis for closer integration of several modern research directions, as discussed with reference to problems of anticipation, neuronal homeostasis, and the interaction of graded and field transmission effects with structured network activity in the brain.

Keywords: anticipation – dominance theory – functional states – homeostasis – parabiosis – lability – Ukhtomsky A.A. – Wedensky N.E.

1   Introduction

The paper focuses on the problem of anticipation in A.A. Ukhtomsky's (1875-1942) theory of dominance and the works of his neurophysiological school in the context of recent developments in related fields. First, the basis of Ukhtomsky's research in the fundamental investigations of his teacher N.E. Wedensky (1852-1922) is briefly outlined regarding functional state dynamics in biological systems. Ukhtomsky's work on the dominant is then introduced and related to recent advances in several areas of neuroscience, including problems of anticipation, neuronal homeostasis, and the interaction of graded and field effects with spike structured neural activity. It will be shown that while in Western neuroscience, the problem of neuronal homeostasis has become an important research topic only in recent years (and mainly with respect to specific signaling pathways), the same and related problematics have been intensely studied by a longstanding tradition of

A. Kurismaa (✉)
Department of Philosophy and History of Science, Faculty of Science,
Charles University in Prague. Viničná 7, 128 44 Praha 2, Czech Republic.
e-mail: andres.kurismaa@gmail.com

Russian/Soviet research. This tradition has incorporated not only specific mediator-related effects and signaling pathways, but also dynamic and electrotonic aspects of homeostatic phenomena into a large-scale systemic framework. Its historical and evolutionary approach remains original even considering recent works that attempt to relate neuronal homeostasis to the notions of non-equilibrium dynamics and criticality. These modern aspects are discussed after the approach of Wedensky–Ukhtomsky school to temporal factors in biological systems (section 2) and their non-equilibrium dynamics related to dominance (section 3) have been introduced.

2 Temporal Variability as a Functional Factor: On the Physiological Approach of the Wedensky-Ukhtomsky School

The modern context for analyzing the problem of anticipation and temporality in A.A. Ukhtomsky's theory of dominance is highly diverse and interesting. On the one hand, interest in evolutionary developmental and behavioral neuroscience is on the rise and has never been more active [1], and shares basic concerns with the dynamic and evolutionary orientation of Ukhtomsky's school (as well as other Russian/Soviet traditions, see [2]). Within cognitive neuroscience, the problems of multiscale temporal dynamics and "time-based" information coding schemes are becoming increasingly prevalent [3-5], calling for a "new cognitive metaphysics", in addition to methodological and technological advances to reframe existing basic approaches [6]. On the other hand, until most recently the question "what are the temporal dimensions of cognition?" has hardly ever been asked by cognitive neuroscientists, "possibly because it appears as either trivial or meaningless" [4], and systematic frameworks to investigate or even pose it seem to have been lacking [3].

> The problems cognitive neuroscientists try to solve are poorly defined on both the cognitive and neuroscience sides…. In the analogy to Plato's cave, our current approach to understanding the biological foundations of cognition is like looking at shadows cast on a region of the wall of the cave without observing how they change dynamically over time /…/. Time is a factor that is often *though not always* ignored in human cognitive neuroscience, and yet several considerations suggest that neural systems may use time as a factor for information coding, processing, and transmission [3, p.1-3, original emphasis].

This paper proposes that perhaps one of the most comprehensive attempts to analyze biological and neurocognitive processes in terms of their temporal dynamics has been made by the neurophysiological school of Ukhtomsky. Ukhtomsky's theory of dominance is noted as one of the most substantial neurophysiological generalizations of the 20th century, as well as grounding fundamental principles of physiological investigation in general [7, p.3]. Considering both the theoretical scope and applied significance of this line of research, it was stated by the well-known neurophysiologist academician A.S. Batuev nearly half a century after Ukhtomsky's death that "the

Fig. 1. Alexei A. Ukhtomsky, Nikolai E. Wedensky.

whole scientific work of Ukhtomsky least of all belongs to history: in its scientific-conceptual insight it surpassed its own time to the extent that he's our contemporary, whereas the real assessment of some of his ideas and positions remains even now a task for the future" [7, p.3]. This remains the case also for the problem of anticipation in biological and cognitive systems [8-11], as argued below.

Recent work has highlighted important parallels between the dominance concept and synergetics, which it anticipated in many respects [12], as well as the prefiguration of Soviet cybernetics by Ukhtomsky's research [13]. The dominance concept drew on the latest developments in numerous contemporary areas ranging from theoretical biology to physics – on the natural science side of the theory. On the other hand, in line with the historical principles of neurophysiology advanced particularly by his teacher N.E. Wedensky (1852-1922), Ukhtomsky sought to reconcile these scientific developments with broad systemic perspectives and philosophical problems of life science methodology [14-16]. In his view, founding an integrative approach to studying the organism and its brain activity required a thorough reconsideration of the basic concepts and methods of classical physiology, as well as the traditions characterizing natural scientific thinking more generally. He notes:

> We attempt to understand the organism as a process, in the regularities of its transitions and reorganizations from one moment to the next. However, during thousands of years, scientific thought has been particularly fascinated by solid bodies with their constant properties, as they could be most easily subjected to scientific investigation and prediction. The mechanistic natural science considered as its natural task to see everywhere, including in physiology, only solid bodies and the results of their interactions in the organism.
>
> Where it was by no means possible to reduce phenomena to the static bonds of solid bodies and talking about processes and events was still inevitable, particular interest was developed for cases where two or several opposed processes form a more or less stable equilibrium, constantly reestablishing itself. Although we are no more dealing here with a solid body with stable properties fixed once and for all, it's still a combination returning to the initial state sufficiently quickly to be reckoned as an extremely close approximation to a solid body with stable properties.… In both cases – in reducing events to the laws of solid bodies and in reducing them to equilibrium laws – what was tempting was specially the possibility of understanding phenomena outside of and independently of time. Establishing constant regularities that are not dependent on time seems like the deepest task of knowledge. This tradition of essentially *ahistorical* science, going back to ancient Greeks and naturalists from

the Renaissance to the XVIII century inclusively, continues to live on to a significant degree among current day physiologists, often unconsciously, in other cases with methodological vigor [15, p.126, original emphasis].

Ukhtomsky notes that since the early 19th century, classical physiology began to increasingly draw on evolutionary theory and its subfields in explaining biological functions, and respectively, focus on the role of time on the macroscopic scale of living processes and nature. The formation, modification, and disappearance of species and ecosystems shown by paleontological evidence were indicative of changes occurring on an irreversible and singular timescale. At the same time, however, the view that physiological functions could proceed under the immediate dependence of currently given temporal conditions and their variations in the microintervals of time would still remain largely neglected at the period. Thus, the tasks of the new physiology as envisaged by Ukhtomsky comprised two essential factors: first, to expand the field of experimental and comparative physiological investigations to the whole of animal and plant kingdoms in studying the genesis of functions; and secondly, to introduce the historical method with particular reference to microintervals of time as fundamental and irreversible constituents of macroscopic temporal events in biosystems [15, p.128].

> As the events of life always proceed with irreversible succession, equilibrium and reversibility play a secondary and subservient role, and the biologist is still forced to reckon with time as an independent factor not subject to any exception. Therefore it is not so much schemes of equilibrium and reversibility that have a real meaning for the physiologist, as the *relative speeds and intervals of processes* realized in the organism. /…/ Where we speak about the *periods and rates* of interrelated reactions, their duration enables to distinguish *measurable intervals, the relative congruence or divergence of which in the cooperating tissues and organs predetermines the events which occur in them* [15, p.129, original emphases].

In this view, different physiological mechanisms could be elaborated in the same substrate by introducing temporal variability into their working intervals. With respect to brain functions, Ukhtomsky highlights in particular that "It would be naïve to think that physiological integration is always and everywhere achieved only through synchronization in neural circuits", as often considered; "more often than not it has to operate by coupled inhibition, i.e. by increasing the temporal divergence of excitation in individual units of the functioning system" [16, p.277]. Thus, the brain's capacity to control and regulate physiological processes requires it to simultaneously "synchronize rhythms in certain elements, while increasing their heterochronia in others" [16, p.275]. This fundamental type of coordination, expressed in temporal and spatial asymmetry or gradient formation between physiological units' activity is central to the principle of dominance, and will be discussed below in detail. Before that, however, the closely related physiological concepts of lability and parabiosis will be introduced.

2.1   *Concepts of Lability and Parabiosis*

Before considering how the above views on temporal variability and its organization relate to the principle of dominance, let us first briefly consider N.E. Wedensky's fundamental research in the late 19th and early 20th centuries which formed its theoretical bases [17]. Here, the notions of physiological state changes and functional (temporal) variability of their work intervals were first established as essentially related, and this for all studied organismic processes. As the founder of this line of studies, Wedensky demonstrated for the first time that physiological responses to stimulation of various nature, duration, rhythm, and intensity reflect general

biological regularities present in any excitable and conductive system as it passes through different functional states in the course of work. It was shown that essentially similar phase transitions occur in the reactivity patterns of various excitable and conductive systems, such as nerves, muscles, glands, and the spinal cord, in response to different stimulation patterns either by chemical (ether, cocaine), physical (constant current) or mechanical means. This indicated both a striking regularity underlying physiological responses in different types of systems, as well as a wide variability and dynamism of their reactions depending on particular conditions of functioning. This approach relegated the static concepts of classical physiology to a secondary and derivative role, e.g., as expressed in the exclusive focus on the "all or none" principle of impulse conductance, particular rhythms as stable properties of organs, and the decomposition of the organism into isolated systems. As opposed to that, Ukhtomsky summarized the results of Wedensky's research as indicating most generally that the "normal physiological operation of any given organ or tissue is not a statically determined value, but a reflection of its current functional condition" [16, p.7].

To analyze the functional states of physiological systems and their dynamics, Wedensky introduced a set of novel concepts into physiology that continue to be employed today (see [18, 19, Tsitolovsky, current volume]). With the notion of *lability*, Wedensky designated the degree of functional mobility/inertia of a tissue as reflected in the speed of its elementary cellular reactions – i.e., the number of excitations or work cycles a system is able to produce per unit of time (1s) under maximum stimulation frequency and with precise correspondence to it. This parameter reflects not only the degree of a unit's resting-state polarization (resting membrane potential), but the ability to maintain this polarization under (intense) working conditions and stimulation over protracted periods (Fig. 2). The opposite tendency or state of *parabiosis* reflects the reduced functional (working) capacity of tissues corresponding to their lowered polarization under stimulation. When reaching the form of stationary excitation (protracted local depolarization), this prevents impulse conductance between regions and reflects a state of tonic inhibition in the excitable or conductive unit. As opposed to lability and heightened functional mobility, the formation of stationary non-propagating excitation corresponds to increased reaction inertia, and leads in the final stages of parabiosis to complete cessation of excitation conductance and reactivity (Fig. 2).
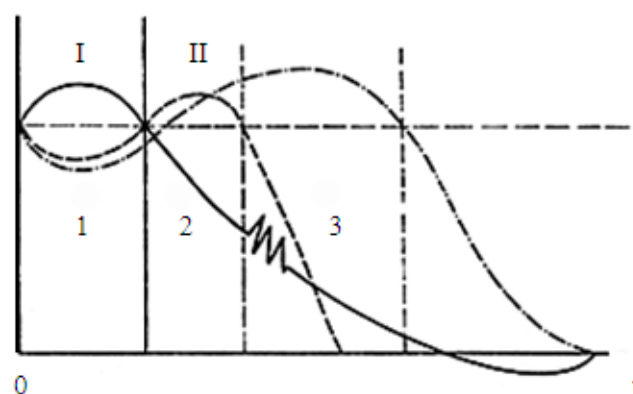

Fig. 2. Schematic depiction of changes in resting state potential, excitability, and reactivity of nervous tissue under conditions of prolonged stimulation and development of parabiosis (inhibition through change of tonic physiological condition; explained in the text). Abscissa – duration of stimulation; ordinate – changes in the functional state parameters of the tissue. Continuous line – change in polarization and lability; dashed line – change in excitability (capacity of non-decremental signal propagation); dashed line with dots – change in reactivity

(ability to produce local potentials). I – phase of polarization and lability increase; II – phase of lability and polarization decrease; 1 – phase of initial excitability and reactivity decrease; 2 – phase of excitation and reactivity increase; 3 – phase of secondary excitability decrease, and the secondary increase and drop of reactivity. As can be seen, the changes of excitability and reactivity follow a parallel course when the level of lability and polarization is high, but diverge in diametrically opposite directions as the latter parameters decrease [20].

It was clear from Wedensky's work that the observed changes in tonic tissue properties cannot be understood in terms of additive superposition of elementary reactions of excitation and inhibition, viewed as isolated events. Instead, complex interference of physiological responses is displayed which grows stronger as the individual waves of excitation follow each-other closer in time and create progressive transformations in the underlying tonic tissue properties. This gives rise to qualitatively and quantitatively different forms of excitation and reactivity in the nervous system in the course of its functioning, and leads to changes in the parameters of lability and reaction inertia.

> Normal, naturally occurring innervation of nervous centers to the periphery and back practically does not know of "single stimuli" – we are almost always dealing with impulse rhythms and response excitation rhythms. For this reason, perhaps, it is more natural and correct to derive the normal features of impulse conductance through tissue not from knowledge about the course of single excitation waves, but from the factual interactions of wave groups and ensembles. We think for this reason that, for example, based on the knowledge of chronaxie or refractory phase from a single wave we can hardly "deduce" the subsequent reaction of the tissue. And we propose that the path of Wedensky, beginning from the study of tetanus and rhythmics, is a more realistic and practically significant path; it is richer in its predictive capacities and penetrates deeper into the factual principles of excitation (Kirzon, M.V., cited in [16, p.188]).

> While classical physiology has in most precise detail studied and continues to study the single action potential, in the conviction that by understanding it we shall have the fundamental key to understanding any kind of excitation complex of whatever degree of complexity since the latter is a product of the combination and superposition of individual waves, we on the other hand observed that individual action potentials both in their magnitude and type of occurrence depend on the position that they occupy in a sequence composing an ensemble. Therefore the regularities which this complex obeys require an entirely separate investigation, given that individual waves are defined in their characteristics as consecutive oscillations in a complex [16, p.188].

Later electrophysiological investigations confirmed [20, references therein] that classical conceptions of excitation as increased spike activity and inhibition as the suppression of action potentials hold true only for the specific, spike structured reactions of nerve centers. Cellular reactivity, in particular the evolutionarily and developmentally earlier graded potentials may not only be retained for a certain period after spike conductance is reduced or lost, but can be amplified in the first moments after action potential propagation has been blocked through progressive parabiosis. These studies allowed to develop Wedensky's conceptions by demonstrating that in the course of their functioning under prolonged working conditions, cells and conductive systems generally exhibit a two-stage change in lability and a three-stage change in excitability and reactivity (Fig. 2).[7]

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[7] It is important to note that parabiotic loss of excitability and conductivity were seen to result not only from strong and prolonged excitation, as an instance of inhibition due to "over-excitation," but also as a possible consequence of omitted or significantly reduced levels of normal stimulation (reduction of normal "trophic" weak background stimulation in tissues, organs, and cells necessary for their function). On the other hand, Wedensky did not interpret the occurrence of parabiosis as a necessarily pathological phenomenon. In line with this, e.g., the classical stages of parabiosis were shown by students of Ukhtomsky to be present in the cortical

All that served to underscore the presence of highly complex interrelations between the parameters of lability, excitability and reactivity. These parameters are coupled in time and closely integrated, but cannot be collapsed into a single dimension of excitation/inhibition, nor be treated as all-or-none phenomena as common even in current modeling. As opposed to that, Ukhtomsky and colleagues sought to demonstrate the significance of temporal integration in neural processes, and more generally, the role of reaction history for explaining any physiological function. Present-day modeling based on dynamical and complex system theories allows to corroborate this position and offer it new, more rigorous descriptive tools. However, it seems important to consider that the underlying physiological mechanisms and biological specifics of the observed phenomena remain largely unaddressed by the concepts and frameworks of current theoretical neuroscience [21]. On this background, Ukhtomsky's views on the nature of temporal parameters as organizing factors in biological activity seem no less interesting today than when they were first formulated. Thus, with respect to normal lability changes in tissues, he writes:

> For Western sciences the time of excitation onset (chronaxie) plays mainly the role of a constant characterizing one or another tissue. In lability we see a coefficient that not only changes in the course of reaction, but a coefficient which through its modifications defines in principle the nature of ongoing reactions in the tissue. Western scientists look for conditions in which "temporal parameters" such as chronaxie would change as little as possible. The school of Wedensky directs all its attention at the *laws of normal lability changes*, holding the view that shifts in lability represent the defining factor in the course of ongoing reactions [16, p.143, original emphasis].

In the following, the notions of functional state changes addressed above will be related to the problem of dominance, considered as a basic working principle of nervous processes and their coordination.

3 Problem of Dominance

It is of particular interest in the context of anticipation that regarding physiological lability changes, it was first shown by Ukhtomsky and colleagues that functioning does not necessarily lead to decreased work capacity and functional state of the tissue [16]. In many instances the reverse could be proven to occur: in the course of activity, the tissue gradually assimilates higher frequency rhythms associated with the mobilization of its energetic and metabolic reserves and resources, and thus increases its lability during its exchange with environment.[8] This occurs to the degree that *the physiological processes of work and activity were understood by Ukhtomsky first of all as self-optimizing and autocatalytic phenomena, which potentially increase the non-equilibrium properties of the biological system in the course of its own operations.*

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reactions and decreased physiological lability states of sleep-induced cortical inhibition. Studies also indicate that, at least in its early stages and as a transient systemic inhibition, functional parabiosis can occur as part of normal activity with possible adaptive significance in the sense of leading to increased tissue resilience and range of functional capacities after the temporary parabiotic inhibitory effects are overcome, e.g. in the course of work and excercise (Cf. L.P. Pavlova's "Individuality of Brain Dominants" and respective diagrams therein, current volume).

[8] Cf. respective diagrams in L. Pavlova's "Individuality of Brain Dominants," current volume.

This was seen particularly as a characteristic of the physiological state (or rather, process) of dominance, described by Ukhtomsky in one of his last papers as "*a disruptor of equilibrium, as well as a restorer of work capacity in the very energetic meaning of the word*" [16, p.209; our emphasis] – a condition that is simultaneously characterized by maximal capacity of high-frequency impulse assimilation [15, p.269]. One of the leading, although often implicit questions underlying this problematic was expressed in the same paper – possibly reflecting the influence of one of the founders of Soviet theoretical biology Ervin Bauer[9] [22]: "*If a condition was physiologically and physico-chemically possible where a state of higher potential would also become a more stable state…, it would be incomparably easier to understand the quick return to this stable equilibrium [after each excitation interval], even though it has a higher potential*" [16, p. 225; our emphasis].

> In the central nervous system we have an occasion which violates the principle of least action. It's entirely probable that an individual action potential, once already initiated either in a single neuron, an isolated nerve trunk, or a separate myofibril, will normally proceed according to the scheme of least action. In the following moment after an impulse has occurred, however, the forced process of potential restoration sets in with the absorption of energy from the environment, and the total working effect can accumulate for as long as necessary until there is no exhaustion…. What concerns the organism on the whole, of course the higher the excitation is, the higher also the expenditure and decrease of potential – however, in normal circumstances, the higher also becomes the forced process of restoration, accompanied by the absorption of energy from the environment. How distinct from "least activity"! And first of all, is the organism strictly speaking a closed system in the course of its work? And if it's true that the "organism strives towards equilibrium with its environment", then how profound and voluminous would this environment be in which the organism finds its equilibrium and state of rest?

> The nervous system begins not at all from the least action as a received given, it arrives there as an achievement in the end, and only to initiate new action, face new tasks, new struggle with resistances. /…/. It is all about the question how strong is the dominant that governs behavior. /…/. From a general biological perspective we understand that dominants with their expansion lead to development, enrichment of the organism with new possibilities, and lie at the basis of forming novel reactions [16, p.79-80].

In the physiological definition, a dominant refers to the focus of heightened excitability which temporarily determines the nature of the body's responses to internal and external stimulation. It is based on the concentration of excitation into a certain group of centers which simultaneously inhibit other regions and prevent them from reacting to stimuli that are adequate to them (at least to the extent this interferes with realizing the reaction of dominant centers[10]). This is in principle not an economical process as Ukhtomsky notes, since this type of inhibition

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[9] As testified by Ukhtomsky's close younger colleague I.A. Arshavsky [23], Ukhtomsky was aware of E.S. Bauer's (1890-1938) work, although did not refer to it in this paper, nor in his lectures devoted to the problems of biological equilibrium. At the same time Bauer's work in this area was groundbreaking and remains of significant interest [24, 25]. It voiced similar problems and shared some important ideas with Ukhtomsky's own research (cf. the problem expressed in Ukhtomsky's quote above). Arshavsky, perhaps under the circumstances of his time, expressed surprise over this fact. We know today that Bauer was arrested by the NKVD and executed in 1938, and his works disappeared from Soviet libraries. Ukhtomsky himself had been arrested at least three times by then with serious charges [cf. L.V. Sokolova, current chapter].

[10] "The concept of "collateral inhibition" in dominants should not be distorted. This is not a suppression of any activity at the inhibited sites, but its transformation more or less in line with the dominant direction of activity. The local reflexes can be entirely retained in these conditions: as I'm reading a lecture, without noticing it, I wave off a fly" [14, p.249].

is achieved through a conflict and competition of excitations between centers with various degrees of lability and excitability, often belonging to different levels of the nervous system responsible for different and incompatible functions. In order to realize any one of them, all other possible reactions in remaining centers need to be temporarily excluded from the working constellation.

For clarity, we can consider some simple cases of dominance-based coordination. These were studied in detail by Ukhtomsky and his students while elaborating the first electrophysiological, pharmacological and hormonal models of dominance:

> When the dominant consists of accelerating the act of swallowing water poured into mouth, distant excitations not having immediate relevance to swallowing will stimulate it, and not produce the reaction in their immediate pathways (Ukhtomsky 1911). When the dominant consists of the embracing reflex of frogs in spring, remote painful stimuli, for example in posterior limbs, will evoke a clear reinforcement of embracing with impediment to other immediate reflexes. When the dominant consists of heightened excitability of the sensory centers in the lumbar region of the frog's spinal cord, then most remotely located stimulation of the animal's skin will evoke a rubbing reflex in its posterior limb, directed as if the stimulus had affected the skin of lumbar dermatomes [Ukhtomsky 16, p.34].

This type of coordination cannot be an economical process in Ukhtomsky's view particularly in case the final working effect is realized with the dominance of highest cortical centers (as typical of man) possessing the highest physiological lability and working capacity in the nervous system. Here, "life is clearly "wasteful", expansive", and far from obeying the equilibrium law of least action [16, p.79]. Further, dominants integrate "tonic", non-specific transmission and specific synaptic system effects, which means they are generally protracted innervations with relatively long intervals due to the metabolic and energetic "restorative" processes – in Ukhtomsky's view, primarily autocatalytic and negentropic processes – that follow and are coupled to the abrupt activity of fast action potentials.

Ukhtomsky considers that the most characteristic physiological expression of dominant innervations can be seen in perception and anticipation over long intervals when the organism is required to maintain a protracted working state and oppose the transient reactions evoked by immediate and proximal environmental influences (i.e., overcome the conflict of longer and shorter interval excitations). This requires an ongoing balancing of differently directed processes in the nervous system through a fine regulation of their lability: "Excitation spreads extremely fast within the boundaries of a dominant focus ("center" or "system") and relatively slowly beyond it" [26].[11]

It is significant that over time, Ukhtomsky came to increasingly stress the importance of an optimal level of lability as a prerequisite of dominance and thus to speak of the ratio of optimal excitability to optimal lability as a characteristic of dominant states [27, 28, 20]. "I have always been cautious not to ascribe strong excitation to dominants", writes Ukhtomsky, "it's not the rate of excitation in the center at the moment an extraneous impulse arrives, but the ability to amplify (accumulate) its own excitation state through extraneous impulses that makes a center dominant." While being highly excited, the physiological unit can be in a state of excitatory tenuity, not sufficiently intense and stable to propagate its activity to other centers and thus function as an integrative physiological unit. Respectively, "the problem of dominance would lose all its interest" if it could be reduced to differences of excitation strength between "dominant" and "subdominant" excitations [16, p.53], as opposed to the systemic changes of

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[11] Citations given through [26] refer to Ukhtomsky's archival materials and notes.

polarization and excitability denoted by inter-areal lability dynamics (Fig. 2) [cf. Pavlova, current volume].

The high capacity of rhythmic assimilation defining dominant states is thus a complex property – it marks at the same time increasing work capacity of a substrate during its activity, and an increasing ability to resiliently return to its initial "operative resting" state of readiness for renewed action after each completed work cycle. "Increasing work capacity and the capacity of maintaining steady resting state represent two sides of the same biological achievement" [16 p.175], as physiological rest implies not a passive state of inactivity, but a specifically maintained and highly constrained form of excitability.[12] This is expressed in the ability *not* to react (diffusely) to the mass of indifferent environmental stimuli that continuously surround and fill the organism – or when reaction is necessary, to keep it at its minimal necessary duration, i.e. as labile as possible. This is an evolutionarily and developmentally late ability and achievement.

How does this increase in excitation thresholds accompanying the increased lability of the resting state relate to dominance? As mentioned above, dominance is most clearly expressed in protracted working states – but it is also characterized by heightened excitability (if not strong excitation) in comparison to operative rest. The answer to this seeming contradiction is a highly interesting one, and reflects the complex nature of dominants as non-equilibrium formations:

> The very state of physiological "rest" is a state of protracted tension: during this period the resistance to electric current is highest, the polarization level is highest; maintaining this state and the structural cell surfaces which subserve it requires the largest amount of energy being spent on these "forced" processes. On the other hand, the action potential itself is related to depolarization, decreased resistance, breakdown and parabiosis.

> I would say that dominants form and achieve their highest tension namely during periods of physiological rest, whereas during the realization of "excitation" they are basically run down and dissolved. It's another question whether in such conditions they obtain secondary reinforcement, in the form of exercise, by attracting towards them the greatest amount of nutrient materials [26, p.108].

As the basis of dominant states, Ukhtomsky does not refer to a single dimension of physiological activation in terms of excitation, as was seen above, but to a process and effect of coordinating different types and intervals of transmission – including spike activity, graded and electrotonic potentials, and metabolic processes associated with humoral activity. Some of these aspects were investigated in detail by one of Ukhtomsky's notable students N.V. Golikov (1905-1988) [20]. Based on intracellular and other electrophysiological recordings of his laboratory, Golikov concluded that processes of interneuronal transmission depend on systemic joint effects of both specialized synaptic mechanisms' additive influences and the regularities of non-specific reactions. The latter underlie the stages of tonic transformation in neurons under any kind of stimulation (Fig. 3).

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[12] As a more specific point, there is obviously no such thing as zero activity in physiology, notes Ukhtomsky in his criticism of the all-or-none principle widely used for modeling neurophysiological processes both in his own days and currently. "We are surely to welcome the time when the physiology of excitation will become a mathematical science. It's in this regard necessary to say in advance, however, that the mathematical construction of a theory of excitation on the basis of the "all or none" postulate will remain a particular and exceptional theory, similar to Euclidean geometry. Future mathematical physiology can not avoid the task of measurements within an "elementary excitation". It complicates our conceptions, but in return brings us closer to what exists in nature." [16, p.109]

A large number of facts shows that the specifics of stimulating agents and receptor structures can accentuate or prolong one or another phase of the general (non-specific) cellular reaction to stimulation. /…/ Under prolonged stimulation cells and fibers undergo a two-phase change of lability (rise and fall) and usually a three-phase change of excitability (fall – rise – fall). The three-phase changes of excitability correspond to the development of primary adaptive hyperpolarizing inhibition (anelectrotonic syndrome), subsequent excitation (cathelectrotonic syndrome), and finally transition to secondary depolarizing inhibition (cathode depression syndrome) [20, p.7].
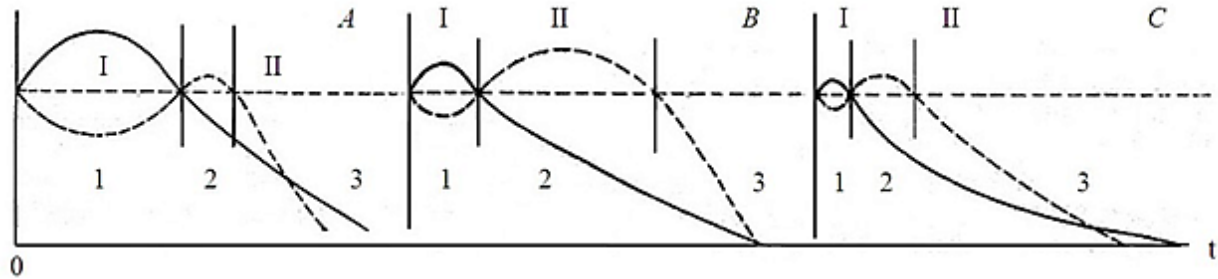

Fig. 3. Schema showing the changing relationships of polarization, lability, and excitability in nervous tissue under prolonged stimulation. A, B, C – influence of agents accentuating and protracting one or another phase of the non-specific reaction. A – influence of "tranquilizing" factors (anode, mild heat, calcium ions); B – influence of "excitatory" factors (cathode, caffeine, phenol); C – influence of "inhibitory" factors (depressant drugs). Abscissa – duration of stimulation, ordinate – changes of polarization and lability (continuous line) and changes of excitability (dashed line). I – phase of lability and polarization increase; II – phase of polarization and lability decrease. 1 – phase of primary excitability decrease; 2 – phase of excitability increase; 3 – phase of secondary excitability decrease [20].

Naturally, the presence and relevance of specific inhibitory and excitatory agents was only confirmed and extended by considering their effects in the framework of physiological state changes.[13] In this view, neither the specific excitatory or inhibitory transmission systems, nor the general type of tonic reactions would be sufficient for explaining complex functions and coordinative processes in the nervous system. To understand them, mutual effects of both types of transmission systems would need to be analyzed:

Materials of evolutionary physiology, demonstrating the development of specific mediator effects from their primary non-specific influences, enable to consider the effects of specialized synaptic structures as accentuations and protractions, predominant expressions of one of the stages of non-specific reactions to stimulation. The activation effects of specialized synapses depend on the level of functional state in the reacting cells. Depending on their polarization level and the degree of lability and reactivity, the trophic effect of a mediator can be replaced by an inhibitory effect, and the inhibitory influence of a mediator replaced by an excitatory effect [20, p.15].

Thus the effects of normal specific reactions can in certain conditions be altered through the general phased regularities of non-specific cellular reactions depending on the cells' functional state. Such complex effects are difficult to explain in the mono-parametric frameworks that have been generally used to study the effects of particular neurotransmitters with no reference to the problems neuronal homeostasis [29], less with respect to the complex dynamic and critical properties this is now found to exhibit [30, 31]. Golikov's results substantiate

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[13] Ukhtomsky made it clear early on in his work that the non-specific inhibition seen in the phases of parabiosis cannot be the sole source of inhibitory mechanisms in the brain (in spite of Wedensky's earlier insistence to the contrary).

Ukhtomsky's early conclusion from a variety of experiments with mediators that the actual *excitatory or inhibitory effect in the system is not exerted only by the mediator itself, but by the shift of lability which occurs under its influence* [16, p.250]. While respective results will require separate presentation and analysis, we can cite several cases discussed in Golikov's work to consider the nature of such effects:

> In the first days of postnatal development, the crossed primary hyperpolarizational inhibition in two-neuron reflex arcs is not yet present in kittens; instead of inhibition an excitatory effect occurs, and only in subsequent days does the inhibitory effect set in together with the increased level of lability and polarization of motor neurons. /.../ The normal inhibition of heart-beats through vagus nerve stimulation is replaced by the accelleration and increase of heart function by the same stimulation in a weakened or dying heart [20, p.8].

Such effects cannot be taken to represent only exceptional (e.g., pathological) phenomena, as variations in normal polarization level are widely present in different neuronal groups and in the dynamics of their reaction to stimulation also within normal physiological limits [20]. This is also evident in dominant states, the dynamics of which express normal, coordinated excitability changes in the brain.

4   Modern Perspectives on Dominance Studies

The above results and conclusions may be of considerable interest in the context of current theoretical neuroscience. We will consider this first with respect to modern studies on neuronal synchronization through the graded effects of local field potentials. These represent fluctuations in the electric fields around neurons resulting from summed transmembrane currents from multiple nearby cells.

Commonly, the electrical fields produced by neural activity have been viewed as a measure of that activity rather than as a mechanism for influencing it [32]. While neurons are certainly to some extent sensitive to the weak electric fields which their physiological activity generates, it has remained unclear whether these fields can have significant functional effects. Generally, they have been assumed to be of relatively negligible influence and nonspecific [32], since weak electric fields (<5 mV/mm) polarize neurons only to a minor degree.

However, recent work has given direct evidence that cortical local field potentials can contribute to the synchronization of the very structured network activity that generates them [33, 34]. This was also Nadin's [35] hypothesis. It is concluded that through the subthreshold modulation of network excitability, endogenous field effects may guide network activity by affecting spike timing and synchronization [33]. This would also have an effect on the time-based coding schemes involved in the spike-phase coding mechanisms recently discovered – i.e., conversion of the excitatory drive in individual neurons into a phase value relative to the local field potential [32]. These and similar results demonstrate a stark contrast between the small amplitude of the weak (yet globally distributed) perturbations at the level of individual neurons and the effects this perturbation can have on macroscopic network dynamics. Neurons are indeed capable of synchronizing their activity to weak electric fields even well below 1 mV/mm, and sensitivity to field effects appears to become more pronounced in neural networks in comparison to single cells
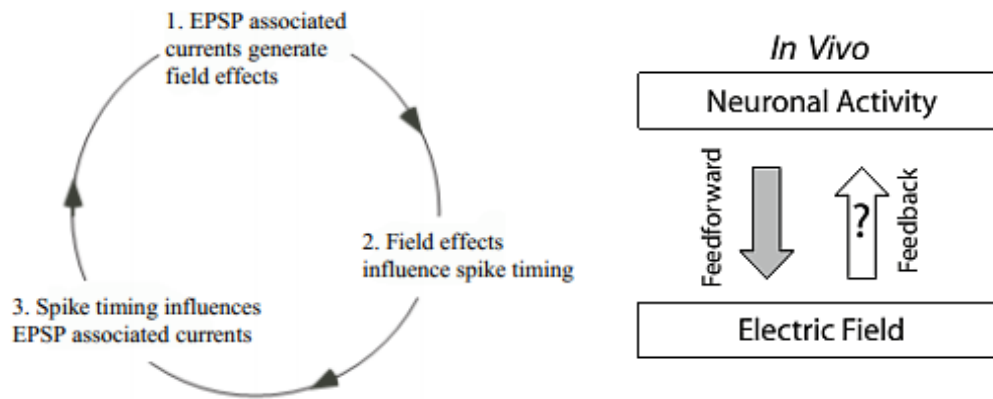
Fig. 5. Conceptual schemes showing feedback coupling between structured neuronal network activity and its underlying endogenous electric field. The timing of spike activity (''feedforward'') influences excitatory postsynaptic potential (EPSP) associated currents, the field effect of which feeds back to structured network activity via spike timing modulation, thus amplifying the network's original spike-associated field effect. By these means, local field potentials may contribute to synchronization of the very network that generates them, and consequently affect chemical synaptic transmission. Schemes redrawn from [32, 33].

[36].[14] These results are seen as opening a new chapter in the study of network synchrony and the place of field effects in neural signaling [34].

As summarized above, dominants were understood precisely in this sense as subthreshold excitation states – not necessarily expressed directly in increased spike rates, but as serving a coordinative role through the regulation of inhibition and excitation in brain networks based on non-specific graded and electrotonic influences. By applying (perhaps for the first time) the theory of non-linear oscillations to the study of neurophysiological processes, Ukhtomsky substantiated this possibility theoretically and noted that, in terms of their excitation rate, dominants may be minor in strength, provided they give stable and consistent signals to entrain higher-frequency rhythms, and this entrainment would enable them to guide macroscopic brain dynamics [16, p. 187-195]. The consistency of this hypothesis with modern results is noteworthy, and may be relevant for yet other aspects of dominance theory which bear directly on the problem of anticipation.

Wedensky wrote in his last letter that it's impossible to construct the "principal foundation" for the general theory of excitation until the influence of electrotonic effects on living tissues has not been elucidated down to its details [37, 38, p.152], and Ukhtomsky shared this view entirely. This concerns ideas that are still new, and relate both to anticipation and basic problems of central nervous system physiology: "*It's the problem of physiological signalization along the nerve still prior to the development of an excitation wave with Helmholz conduction speeds… about electrotonic effects along a nerve over a distance… with speeds that significantly exceed those of Helmholz*,[15] wrote Ukhtomsky [38, p.162]. Although lacking the technical means to prove it at the time, Ukhtomsky formulated the idea that brain structures are

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[14] These findings also indicate that the observed modulatory effects on neuronal excitability are not restricted to particular structures where non-synaptic modes of transmission are known to play an important role such as the hippocampus, or to clinical conditions of pathological activity where susceptibility to very weak field effects had been found earlier (e.g., in the hyper-excitable and pharmacologically activated rodent hippocampal networks). Current results indicate weak field effects may generally have a fundamental role in defining the activity of structured neuronal networks through the subthreshold modulation of their excitability [34].

[15] This refers to the speed of normal action potential propagation along a nerve fiber, as first measured by H. von Helmholz in 1849.

able to send an anticipatory signal to the effector before the subsequent spike excitation arrives, and this would enable to "prepare the effector in advance, inform it about the consequent arrival of impulses" [38, p.164]. Later experimental work by his students confirmed this idea, e.g., by showing the presence of distant electrotonic effects in a frog's heart by ECG analysis with heart bridge [39]. Unfortunately, we are not aware of further work in this regard pertaining directly to anticipation – as opposed to the formation of "temporal associations" (i.e. conditioning) under the influence of dominants induced through electrotonic states. The latter work was conducted by Ukhtomsky's younger colleague V.S. Rusinov in the framework of his polarizational-electrotonic model of dominance [40], which investigated in detail some of the graded and electrotonic field effects underlying dominant states.

The reason for the above limitation may be due to the experimental difficulties which still remain in defining and antagonizing respective field effects. Currently, authors also call for caution "in assigning functionality to biophysical mechanisms in neural systems" [32], regardless of the increasing recognition of their potentially central role in coordinating and organizing structured network activity [33, 34]. It's in this regard interesting to note that respective work by Wedensky, Ukhtomsky, and their students did not consider electrotonic and related field phenomena as solely physical phenomena, but as physiologically specific states reflecting the functional condition and its changes in neural systems [39], and as indicated above – with a possible anticipatory functionality.

This interpretation may be valuable also in the context of current research on neuronal homeostasis. We saw that Ukhtomsky's work, and particularly those of his later students like N.V. Golikov, are interesting as they enable to see the properties of various non-specific reaction types in relation to specific mediator effects. Although these results will require separate detailed analysis, we can highlight several significant facts and points of contact with current research. By bringing together ideas of neuronal homeostasis (neuronal functional states) with notions of non-linear state transitions and oscillatory systems, Ukhtomsky can be seen as ahead of the theoretical neuroscience of his time to the extent that the studied phenomena seem to remain largely unaddressed even in today's research.

> The concept that inhibition arises from excitation, which is analogous to phase transitions in contrast with inhibition due to structurally fixed inhibitory substance, permeates all aspects of the teaching of Wedensky and Ukhtomsky. This teaching has thus far encountered difficulties and lack of comprehension because of the quite complex, poorly understood, and often paradoxical physical manifestations of the phase transitions which underlie it [42, p.239].

At the same time as currently noted, it's in fact no less than "shocking to realize how recently neuroscientists started to concern themselves with the problems of homeostatic regulation of neuronal excitability and network function" [29, p.161] – mainly in the last decade – considering how fundamental properties of any living system homeostasis reflects, and for how long and extensively it's been studied in other areas of biology, including the neuroscientific schools of Russia and Soviet Union [16, 18, 20, 37, 40, see L. Tsitolovsky, current volume].

This holds similarly with regard to the novel lines of dynamical modeling of the brain as a critically balanced system. It is currently a major challenge to understand the exact physical and biological mechanisms by which the brain arrives at and maintains criticality [30, 31] – a meta-stable condition associated with numerous optimality criteria for information transmission and functional properties. Criticality has been shown to have close parallels to how Ukhtomsky interpreted dominants as non-equilibrium formations close to a phase transition [42]. Until the last few years, however, predictions of criticality have remained untested in real living brain

tissue in Western research. Specifically, "experiments on the in vivo homeostasis have not yet been performed with attention to the possibility that criticality may be the end goal of homeostatic processes", and current studies are taking first steps towards understanding how cortical function and dysfunction may be tied to criticality and loss thereof in the brain [30].

The global control and critical balancing of the spread of excitation and inhibition in the brain is currently seen as an emergent property in a hierarchy of biochemical regulatory systems [43] operating at various levels of cellular networks, individual cells, and subcellular domains. The emergent nature of this regulation is particularly highlighted by cases where similar network functions have been found to arise from widely divergent underlying mechanisms, in a similar manner as in single neurons closely corresponding patterns of activity can result from different combinations of transmembrane currents [44, 45]. Particularly regarding higher levels of analysis, it is observed that an organism's adaptation and survival cannot directly depend upon the strength of single synapses or the precise number of channels in particular neurons. What matters, instead, is the animal's ability to perform integrated functions such as feeding, walking and breathing. It is most likely the simultaneous, coordinated regulation of various large networks that allows the animal to function at such integrated levels:

> It is possible that the target for homeostatic regulation might not be the behavior of individual neurons alone, but also network performance. How might this be achieved? In some cases it is possible that cell-autonomous or local tuning rules might be sufficient to produce adequate network performance. For example, if the [lobster] stomatogastric ganglion is deprived of its neuromodulatory input it first loses its ongoing patterns of rhythmic activity, then, subsequently (over days) its rhythmic activity returns. This recovery is associated with increases in excitability in individual network neurons, as channel expression is altered. In this case, it could be sufficient for each neuron to modify the densities of its own ion channels and receptors using a cell-autonomous target for network recovery to occur. However, in other cases, adequate network performance might require an as yet unidentified global sensor of network performance to provide error signals for the tuning of the network [44, p.571].

The study of coordinated changes regulating circuit and network homeostasis is just beginning, but there are strong grounds to believe that the mechanisms involved in the maintenance and modification of network excitability are not limited to established cell-autonomous mechanisms [45]. It is of particular interest in this light that V. Rusinov's studies [39, 40] provided direct evidence of large-scale synaptic and neuronal homeostatic changes under the influence of cortical polarizational dominants. Specific histological and histochemical changes evoked by weak constant current stimulation[16] were shown to be associated with this state in the pyramidal neurons, interneurons and glial cells of the stimulated motor zones. Respective ultrastructural analysis revealed significant increase in the number of synapses with a large number of synaptic vesicles in the lower layers of the motor cortex, confirming the increased level of functional synaptic activity in the dominant focus. Further electron-microscopic investigations determined that this increase is also accompanied by changes in both pre- and postsynaptic components of axodendritic synapses [39].

As Rusinov stressed – the various cortical elements in a polarizational dominant react as a unitary functionally organized ensemble or system with long-term effects after the current is switched off. This cannot be explained by shifted membrane potentials, which return to their

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[16] Rusinov induced polarizational dominants by weak constant current (0 to 10×10^{-6} A) stimulation by point electrode. Without evoking any overt peripheral effects in the experimental animal (rabbit), this modified the state of the stimulated (motor) cortical zone, which assumed to the characteristic properties of a dominant [40].

initial levels almost immediately after the current is turned off, and which from the perspective of the polarizational model represent only the first and preliminary effect of forming a dominant physiological system. The dominant focus, according to Rusinov, entails widely integrated structural and biochemical changes occurring under electrotonic effects. Studying the ultrastructure of the axosomatic and axodendritic synapses of the stimulated motor cortex showed that the polarizational dominant is a phenomenon occurring closely within physiological limits, i.e., the observed shifts remain within the range of normal functional changes. At the same time, the organization of homeostatic processes is analyzed here as the basis of new behavioral adaptations and global changes in organisms' response patterns (modelled by conditioned associations), which entails the reconsolidation of widespread brain systems' structural and biochemical stability at a different, higher level of physiological activity.

In addition to extending the problematic of homeostasis from single neurons to circuits and large-scale neural networks, these results obtained within the framework of dominance studies seem of significant interest also considering current attempts to integrate low-level synaptic and neuronal homeostatic signaling mechanisms into models of higher-order decision making and anticipatory behavior [46]. In line with previous discussion, the question of a "global sensor of network performance" providing error signals that tune widely distributed networks' excitability may depend on feedback mechanisms involving macroscopic electrophysiological field processes that modulate and guide structured network activity. This is most likely considering that, in comparison to the electrotonic and graded effects analyzed by Ukhtomsky's school, the various signaling pathways and receptor processes involved in neurochemically specific cellular and network level homeostatic functions are normally assumed to operate relatively slowly and require reliable integration over longer timescales. This requirement is not compatible with abrupt decision making processes in higher-order brain systems which integrate information from widely distributed memory sources in real time to generate predictions and ongoing action anticipation [46]. On the other hand, in the framework of the "cyclic" interaction of graded and structured activity, the proposed global feedback signal could represent a network-wide synchronization mechanism that enhances the spatiotemporal structure of network activity [33, 34], and could correspond to anticipatory modulation of its subthreshold excitation dynamics across various time-scales as proposed in the dominance model [16, 40].

Further research in the framework of dominance theory may also help to bridge research in the above mentioned areas with problems of higher-order neurocognitive functions. This represented a central starting point of Ukhtomsky's own work. Substantial progress has been achieved in this regard in the works of his students and followers, who have experimentally verified the basic principles of dominance and constructed novel frameworks of systemic psychophysiology on this bases. This has been done with particular orientation to human and social psychophysiology (see L. Pavlova; V. Ilyukhina, current volume), i.e. research directions which represent some of the most challenging fields of modern neuroscience. Although the questions of higher neurocognitive functions are essential from the perspective of dominance theory, addressing them goes beyond this paper and will remain a future task.

5   Conclusion

The present work has discussed the theory of dominance developed by A.A. Ukhtomsky in the context of his neurophysiological school and modern research in related areas. The theoretical

foundation of Ukhtomsky's dominance studies is presented in some detail, as this goes back to the fundamental investigations of his teacher N.E. Wedensky on biological systems functional state dynamics, described by the concepts of lability and parabiosis. It is demonstrated that in the modern context, Ukhtomsky's tradition and theory of dominance relate and systematize in an original way several important theoretical problems of neuroscience – as reviewed with respect to the problems of anticipation, neuronal homeostasis, and the interaction of graded and field effects with structured network activity in the brain. It is concluded that due to the particular orientation of dominance theory to systemic understanding of neurocognitive functions, integration of dominance theory into modern research may open up new pathways of integrative neuroscience.

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STUDY 2.

Kurismaa, A., & Pavlova, L. P. (2016). The dominant as a model of chronogenic change: The relevance of AA Ukhtomsky's and LS Vygotsky's traditions for systemic cognitive studies. In: Klempe, S. H., Smith, R. (Eds.), *Centrality of History for Theory Construction in Psychology* (pp. 125-149). Springer: Cham.

Author contribution:
The author conceived the idea and drafted the first part of the paper (7.1 – 7.3), and drafted the second part of the paper (7.4 – 7.5) based on original materials from L. P. Pavlova and his own research.

Chapter 7
The Dominant as a Model of Chronogenic Change:
The Relevance of A. A. Ukhtomsky's and L. S. Vygotsky's Traditions for Systemic Cognitive Studies

Andres Kurismaa and Lucia P. Pavlova

Abbreviations

AG Activation gradient
CAP Cortical activation pattern
EMA Eye movement activity
FMA Focus of maximum activity

Abstract This paper analyses the role of A.A. Ukhtomsky's principle of the dominant in L.S. Vygotsky's psychological theory, as well as the relevance of their scientific schools in the context of current cognitive research, particularly on the dual-process models of mind and embodied cognition. It is proposed that the dominant principle – founded by A. A. Ukhtomsky, and elaborated by L. S. Vygotsky and colleagues, enables to analyze functional reorganizations of cognitive and cortical activity on the behavioral time-scale, thereby further specifying the chronogenic principle of systemic dynamic localization of higher psychological processes during ontogeny. It's shown how the dominant serves as a model of historical (developmental) explanation bridging psychology and physiology, and has the potential to advance shifts in current research directions.

Keywords

A. A. Ukhtomsky – L. S. Vygotsky – Dominant principle – Dynamic localization – Semiotic mediation – Dual processes – Historical explanation

A. Kurismaa (✉)
Charles University, Prague, Czech Republic
e-mail: andres.kurismaa@gmail.com

L. P. Pavlova
St. Petersburg State University, St. Petersburg, Russia
e-mail: karl@lp1884.spb.edu

7.1 Introduction

This paper examines the inter-related works of A. A. Ukhtomsky (1875–1942) and L. S. Vygotsky (1896–1934) on the problem of the dominant, as well as subsequent developments of this theme in the light of modern studies and works of their scientific schools. The framework of the dominant points to an important case where early theoretical resources both influence a continuing scientific program and have the potential to advance shifts in current research directions. First, the paper sets out to show how Ukhtomsky's physiological studies on the dominant influenced important aspects of Vygotsky's psychological thinking, including his interpretation of higher and lower psychological processes, as well as their systemic and changing relationships in behavior and development. Further, in line with the dominant model, it is shown how the dynamic localization of higher cognitive and cortical processes can be analyzed from the perspective of their chronogenic change in the course of human activity, which remains a key problem for present-day studies. The relationships of this position to current problems in dual process theories of mind and related work in embodied cognitive science will be considered.

In the context of contemporary psychology and cognitive studies, historically oriented problems, such as temporal-developmental analyses of psychological processes and their intra-individual variation, have remained unduly neglected until recently (Molenaar 2008; Molenaar and Campbell 2009; Cohen 2011). Addressing them seems to require extensive rethinking of existing methodologies both in developmental sciences and psychology (Overton and Molenaar 2015), as well as cognitive sciences more generally (Stotz 2012; Molenaar 2008). In the systemic approach to human psychology and psychophysiology considered in this paper, the above questions are analyzed with respect to the temporal formation of working dominants (dominantogenesis) in human higher cognitive and cortical functions (Pavlova and Romanenko 1988; Pavlova 2016). In particular, it is shown how the model of the dominant enables to apply Vygotsky's and A.R. Luria's principle of chronogenic localization of psychological processes on the behavioral time-scale, and can thereby be further integrated with A.N. Leontiev's approach to the macro- and microstructure of activity. On this basis, a systemic framework for the study of human cognition can be founded which addresses key questions of current research.

7.2 The Problem of Chronogenic Variation

The legacies of Ukhtomsky and Vygotsky intersect along numerous lines. In the following, mainly those will be addressed which most closely relate to the problem of historical explanations, and in particular, to the problem of chronogenic change in the structure, function, and localization of higher psychological processes as they undergo (micro)developmental modifications in the course of human activity and development. We are particularly interested in the problems of learning, practice, and skill formation as instances of mastery over particular activities and forms of higher psychological processes in the sense of Vygotsky's historical school. Such mastery seems to entail qualitative changes in the system of higher, semiotically

mediated psychological functions, as well as in their relationships to more elementary biopsychological or non-mediated forms of cognition.

Although related questions belong to the center of the cultural historical theory, they seem to have remained insufficiently studied and understood. This is particularly so from the perspective of neuropsychology and related disciplines (Toomela 2014), including psychophysiology. In the subsequent sections, we attempt to show that Ukhtomsky's principle of the dominant, interpreted and developed by Vygotsky in numerous writings, may be an important basic principle to explain qualitative developments in the organization of psychological and psychophysiological functions. This focus confirms that Ukhtomsky's legacy may help to highlight some essential, if so far unexamined connections between Vygotsky's, Luria's and Leontiev's works (Jantzen 2004); it also agrees with the need to consider the latter's activity theory less as an alternative, and more as a necessary complementary analysis with respect to Vygotksy's and Luria's cultural historical approach (Cole and Gajdamaschko 2007). Before turning to these topics, however, we will briefly comment on the contemporary interest and context of this type of inquiry, as well as examine the close connections between the legacies of Ukhtomsky and Vygotsky in relation to the dominant.

In various areas of contemporary psychology, it is common to raise similar questions and problems to those studied by Vygotsky and colleagues in the framework of cultural historical theory. This is evident in the continued search for dynamic frameworks inclusive of social factors within developmental and embodied cognitive science (Marshall 2009, 2015; Overton & Molenaar 2015; Jordan 2013; Martin 2012). The same parallel also concerns specific hypotheses and agendas. A number of recent experimental findings and theoretical problems have been informed by so-called dual process theories of mind that receive increasing attention within cognitive and social psychology (Evans and Stanovich 2013; Evans & Frankish 2009; Sherman et al. 2014), as well as human social neuroscience (Satpute and Lieberman 2006; Spunt & Lieberman 2014). It seems that related debates have advanced considerably in the past decade, and currently there is substantial empirical and theoretical support to proceed along dual process lines of research (Evans & Stanovich 2013). Interestingly from the persent perspective, what unites this otherwise diverse group of theories and models is the attempt to define, test, and model presumed qualitative differences in various psychological functions in terms which seem to overlap significantly with the distinction between higher and elementary types of psychological processes in the cultural historical tradition. A schema showing some frequently employed dual process attributes is given in Table 7.1, though many qualifications are necessary for interpreting respective (assumed and established) dissociations coherently (Evans & Stanovich 2013).

So far the development of dual process theories and concepts seems to have overlooked this parallel (Frankish & Evans 2009; Sherman et al. 2014), but it seems worth pointing out that the cultural historical tradition spans studies which may still be some of the most extensive ones on the problem of correlating biological and social factors in the genesis of the human mind.[18]

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[18] Interestingly, in a recent historical overview of dual-process theories (Frankish & Evans 2009), the name of Vygotsky is mentioned in connection with his studies on ego-centric speech; and it is referenced in the same context in a recent compendium of dual-process accounts of the social mind (Sherman et al. 2014). The

These studies continue. There has indeed been a large proliferation of works investigating Vygotsky's legacy and school in recent years, including the activity theory of his associate, Leontiev. Nonetheless, no connections between these research agendas and the aforementioned modern frameworks seem to have been examined from either side. This paper can only highlight some possible shared grounds for a dialogue pertaining to the chronogenic organization of functions, considered from the perspective of current (dual process and related) studies on the one hand, and of Vygotsky's school and the framework of the dominant on the other.

Table 7.1. Attribute clusters of some frequently employed dual-process and dual-systems distinctions.

System 1 / Type 1 process	System 2 / Type 2 process
Autonomous / Habitual	Controlled
Nonconscious	Conscious
High capacity	Low capacity
Fast	Slow
Parallel	Sequential
Tacit knowledge	Explicit knowledge
Difficult to alter	Malleable
Low demands on working memory	High demands on working memory
Set of (sub)systems	One integrated system
Evolved early	Evolved late
Similar to animal cognition	Distinctively human
Universal among humans	Varies by individual and culture
Basic emotions	Complex emotions

As well known, Vygotsky and his associates understood higher psychological functions as sociohistorical in origin, semiotically mediated in structure, and conscious and voluntary in their mode of function (Luria 1980, 30). In agreement with the principle of dynamic organization and localization of higher functions, both their structure and localization in the brain are assumed to undergo notable changes during ontogenetic and microgenetic development.

Unfortunately, in comparison with Vygotsky's more general ideas on the sociogenesis of the human mind, his principles of dynamic organization and chronogenic localization of functions

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cultural historical approach as such is not mentioned in either case. We highlight this less as a historical omission and more with respect to the fundamental theory and methodology of related research (cf. Veresov 2010).

have remained much less known in the West (Toomela 2014; Akhutina & Pylaeva 2011; Akhutina 2003). These ideas were clearly established in Vygotsky's neuropsychological writings, but more extensively implemented at a later stage in the development of neuropsychology (cf. Akhutina and Pylaeva 2011; Simernizkaya 1985). Even now, it is observed that the principles of systemic dynamic localization have remained incompletely assimilated into psychological science (Akhutina 2003; Akhutina & Pylaeva 2011; Toomela 2014), and this regardless of their broad implications for theoretical and neuropsychology. Indeed, it seems that without such a perspective (focusing on the developments of both higher and elementary functions), it is impossible to define which psychological processes and units have their origins in the socio-cultural environment and which represent individual biological endowments (Toomela 2014). This is a basic question for human sciences and epistemology in general. The surprising scarcity of such studies, and the relatively little consideration given to Vygotsky's and Luria's neuropsychology may explain why there seems to be almost no further information available to clearly differentiate symbolically mediated higher psychological systems from non-mediated systems, as important as it also is for clarifying the very subject matter and methods of human psychology (as opposed to general biology and neuroscience) (Toomela 2014).

On this background we wish to point out some interesting recent developments, before turning to the problem of the dominant. Within the dual process framework, Lieberman and colleagues have sought to integrate non-mediated and mediated processes into models of human social cognition (Satpute & Lieberman 2006; Spunt & Lieberman 2014). Their work, identifying the so-called reflective (C-) and reflexive (R-) cognitive systems, applies evolutionary, developmental, and behavioral criteria in parallel to understand autonomous and controlled forms of social cognition. This strategy seems methodologically close to one of the leading principles of Vygotsky's school, according to which understanding the operations of a mental function requires restoring, both theoretically and experimentally, the processes involved in its phylo- and ontogenetic development (Luria & Vygotsky 1992). At the same time, new experimental paradigms and methods are proposed to differentiate between the processing modes of the two stipulated systems and model their presumed qualitatively distinct phenomenal, operational, and neural aspects (Spunt & Lieberman 2014). Some hypothesized large-scale correlates of the C (mediated)- and X (non-mediated)-systems are shown in Fig. 7.1. Most importantly, however, and in line with the functional systems approach of Luria's neuropsychology, the authors presume not only that various substructures may need to be distinguished within each depicted region and belong to different systems (C and X), but that a function's mapping to the C- and X-system structures can in some cases chronogenically vary as it undergoes (micro)development (Satpute & Lieberman, 2006). However, work along these lines seems to have only begun.[19]

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[19] There is evidence to suggest, for example, that certain brain regions (such as the MPFC, medial pre-frontal cortex – Figure 7.1) may perform symbolic functions unique to human social cognition, but these functions can to some extent be slowly learned by the X-system structures over time (Satpuke & Lieberman 2006). Such localizational changes have profound neuropsychological implications, as shown particularly in the Luria-Vygotsky paradigm (Vygotsky 1997a, 139-144; Luria et al 1973; Simernitzkaya 1985; Toomela 2014; Akhutina & Pylaeva 2011).
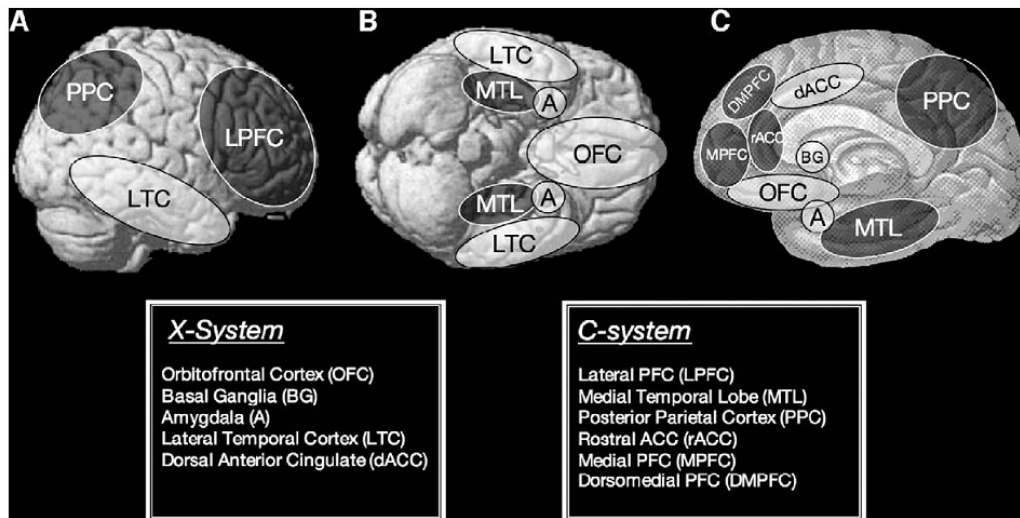
Figure 7.1 – Neural correlates of the C-system and X-system displayed on a canonical brain rendering from (A) lateral, (B) ventral, and (C) medial views (Lieberman 2007; Satpute & Lieberman 2006). Note: the hippocampus, nucleus accumbens, and amygdala are actually subcortical structures that are here on the cortical surface for ease of presentation. Reproduced with permission from Satpute and Lieberman 2006.

In this context, it would seem that joining the evidence and theoretical paradigm of Vygotsky's school with modern dual process approaches could be most productive. This is particularly the case as notable methodological differences may still be present in the way the dynamic localization and systemic structure of functions are understood (Luria 1980; Christensen et al. 2009; Hazin & Tarcísio da Rocha Falcão 2014); furthermore, definitive evidence to distinguish between the symbolic or non-symbolic nature of any given structure have been largely unavailable until now in both traditions. As will be expected, any such attribution will remain conditional, in the sense of being chronogenic, context-dependent and imperfectly aligned (covariant) across functional dimensions (Table 1) (Spunt & Lieberman 2014; Spunt 2015).

Among numerous fields where the question of symbolically mediated and non-mediated functions has major implications, cognitive psychology and its applied areas, such as cognitive ergonomics, stand out. Unlike most of the laboratory approaches to cognition, the study of complex dynamic situations over which human agents exert only partial control offers rare opportunities to study real-time variations in the dynamics and organization of cognitive functions (Hoc and Alamberti 2007). This kind of study has particularly stressed that several cognitive control modes can act in parallel, show quick temporal reversions, and evolve rapidly both in relation to task requirements and human operator states. Nevertheless, modeling and understanding the mechanisms of such complex dynamic processes has remained a central challenge for the field, and new approaches are currently required to better understand various cognitive control types, compromises, and strategies of mental work load optimization (Hoc & Alamberti 2007).

One of the present authors has investigated the above questions from the perspective of Ukhtomsky's and Vygotsky's traditions and developed a systemic psychophysiological framework for their analysis (Pavlova & Romanenko 1988; Pavlova 2016). Before turning to

these studies, however, an outline of the dominant principle and its role in Vygotsky's legacy will be given.

7.3   The Dominant in Vygotsky's Legacy

The shared epistemological background and scientific style of Ukhtomsky's and Vygotsky's research paradigms is notable. Both authors engaged in wide-ranging syntheses of available knowledge and sought to establish new, complex research paradigms on human biosocial nature and development. Each scholar first had a professional background in the humanities before turning to experimental science, and each subsequently elaborated a framework steeped deeply in both naturalistic as well as humanistic traditions and interests. This is no doubt one reason for the continued study and rediscovery of their legacies, though also for the difficulties related to their scientific reception (leaving aside societal aspects of the periods involved).

Given such close parallels, the connections between the two traditions have been surprisingly little analyzed (Jantzen 2004, 2005; Van der Veer & Valsiner 1991, 32-34). Recently, the dominant principle has been reconstructed as an important, if largely implicit, inspiration for Vygotsky's later theories of emotion and personality (Jantzen 2004, 2005). In these studies, Vygotsky formulated the category of "experience" as an elementary unit of psychological processes in a way that seems to find its close psychophysiological counterpart in the similarly monistic principle of the dominant (Jantzen 2004, 2005).

This interpretation agrees also with Vygotsky's early views on the subject. At the beginning of his career, together with several colleagues, he conducted a series of experimental studies on the problem of dominant reactions (Vygotsky 1926; cf. Van der Veer and Valsiner 1991, 32-34). The results of these experiments led him to believe that the structure of human behavior and the unity of experience are generally organized according to this principle. Thus, on the basis of dominant processes, psychological phenomena could be analyzed as integral wholes:

> The simplest rule of the structural unity of our experience seems to consist in the tendency of reactions towards dominance, i.e. the organization of all experience in accord with it; the conflict of reactions for prevalence; the more or less stable predominance of one reaction, based not on the supression of all others, but on the elaboration of a certain resultant, combined effect of all competing reactions. Subordinated reactions are also included in the structure of behavior, but are determined by the leading reaction (Vygotsky 1926, 122).

This formulation followed directly from Ukhtomsky's studies on the dominant as a systemic physiological principle. Ukhtomsky's and his colleagues' research had shown the normal coordination of functions to depend on selective intensification of particular reactions as if at the expense of other, simultaneously inhibited ones. The latter processes are transformed in line with the leading reactions, and at least temporarily assume a secondary, supportive or subordinate relation to them. Ukhtomsky understood this asymmetrical pattern not only in physiological (and psychological) but also general biophysical terms as leading the whole system away from equilibrium dynamics towards higher work capacity necessary for new, increasingly complex (and often energetically "wasteful," i.e., expansive) reaction norms and

functional systems to be established in the developing organism (Ukhtomsky 1978; Pavlova 2016).

In comparison to traditional approaches, the principle of the dominant led to a novel orientation also in the study of psychological and behavioral processes. Instead of considering their dynamics in response to isolated stimuli or events, interest shifted to the role that cognitive processes play in diverting, inhibiting, amplifying, and directing the dynamics of other, subdominant reactions in the organism (Vygotsky 1926, 105). Physiologically, this type of phenomena were already clearly established by Ukhtomsky and his colleagues. However, the psychological mechanisms and structure of dominant processes remained to be further disclosed, particularly with respect to human voluntary activity. To better understand these aspects, we will first consider Vygotsky's analysis of the dominant principle in higher psychological functions. After that, its role in the organization of biopsychological processes will be addressed, including the complex question of their cultural mediation and relations to higher functions.

The crucial point to emphasize from Vygotsky's early experimental findings is that, given a conscious disposition or set, it was confirmed that even an objectively weak reaction could obtain the role of a dominant (Vygotsky 1926). Specifically, his studies showed that in human subjects engaged in simple operator work tasks, the unconditional reflexes evoked by competing or extraneous (collateral electrodermal) stimuli may incomparably exceed in strength the coinciding leading (dominant) reactions, yet remain in a subordinated relation to them depending on the subject's conscious set and voluntary attention, i.e., depending on higher psychological processes (Vygotsky 1926). This emphasis, placed not on the intensity of dominant reactions as such, but on their temporal regularity and (subthreshold) summation, and thus typically slow maturation over time, constituted a central aspect of the dominant concept from its onset in Ukhtomsky's works (cf. Ukhtomsky 1966: 48-63). In Vygotsky's view, it represented a most important theoretical problem for psychology (Vygotsky 1926, 122-124), as neither reaction (stimulation) intensity as such, nor the phenomena of collateral inhibition (of subdominant processes) could clarify the mechanisms and structure of higher psychological dominants.

If in a still far-removed theoretical perspective, understanding this type coordination was expected to lead to the objective study of conscious behavior. In conscious acts, the subordination of isolated reactions to dominants should achieve its most distinct and pronounced forms (Vygotsky 1926). Accordingly, the principle of the dominant could enable the objective investigation of not only the mechanisms by which individual reactions are coordinated in the structure of behavioral acts, but potentially also of the mechanisms underlying human attention, thought, and consciousness (Vygotsky 1926), following Ukhtomsky's own psychological formulations (Ukhtomsky 1966).

In our view, Vygotsky's appreciation of the framework of the dominant should be understood first of all in a methodological light. With the study of physiological lability and variability of systemic functions (cf. Kurismaa 2015), the works of Ukhtomsky and colleagues formulated a methodological principle which Vygotsky considered extremely important and fruitful for objective psychology (Vygotsky 1926, 103): "the normal workings of an organ in the organism are not a pre-determined, permanently settled quality of that organ, but a function of its condition" (Ukhtomsky 1966, 7). From this perspective, Ukhtomsky compared the often

pronounced variability of functions seen in development and behavior to phase transitions of matter that may lead to its qualitative and sudden reorganizations (Ukhtomsky 1966, 7). Most interestingly, in line with this analogy, the dominant regulatory processes in Vygotsky's behavioral psychological study were found to be both stable and continuous within certain critical limits, as well as to exhibit sharp, qualitative transitions between dominant and sub-dominant processes in the course of voluntary behavior when these limits were crossed (Vygotsky 1926).

Depending on experimental conditions, Vygotsky found that subdominant and competing behavioral reactions could even accelerate and intensify the dominant higher psychological process. This confirmed another central aspect of Ukhtomsky's neurophysiological observations and theory (Ukhtomsky 1966, 1978), according to which dominants can be sustained in the nervous system by the stimulation of diffuse (subdominant) excitation waves originating from surrounding brain areas that would normally perform unrelated or competing functions. Now, however, as a result of their stimulation, "it is as if a new potential is infused into the ongoing [dominant] reaction, from which it accelerates on its path and proceeds with greater discharge" (Ukhtomsky 1966, 247). Vygotsky had earlier (Vygotsky 1997c) noted that it may seem paradoxical to assume the possibility of translating these physiological results into psychological form – to assume, for example, acts of (sign-mediated) attention that not only are not weakened by unrelated, extraneous sensory stimulation, but on the contrary become reinforced by it. "That this view is correct is confirmed, however, by a whole series of observations that have yet to be collected into a single psychological law," wrote Vygotsky around the time of his experimental study (for examples, see Vygotsky 1997c, 130). It was this type of regularity or rule which his own study of dominant processes aimed to further elucidate (Vygotsky 1926). We are not aware of any similar demonstrations in current dual-process literature (Spunt & Lieberman 2014, Satputke & Lieberman 2006) or other attempts to study this most interesting question.

The psychological results considered above thus fully substantiate Ukhtomsky's hypothesis about the general role of the dominant in organizing psychological and psychophysiological functions. Its effects are not limited to exceptional cases, departures from an ideal baseline of stationary activity or normal "equilibrated" functions (Ukhtomsky 1966). On the contrary, Ukhtomsky presumed dominant-free states to occur only in rare conditions such as pathological or borderline states of consciousness (e.g., sleep-wake transitions). From what has been considered, all normal human activity – including its higher, sign-mediated forms, may be characterized by the coordination of psychological processes on the basis of their relative dominance. To understand its developmental formation and preconditions, let us briefly consider the genetic methodology of Vygotsky's work.

The dominant seems to assume an important place with respect to the general developmental principles formulated by E. Kretschmer, which Vygotsky discussed at length and elaborated further (Vygotsky 1998). These principles express basic genetic regularities such as the "upward transition of functions" during nervous system maturation and the corresponding "subordination" of lower (evolutionarily older) centers by newer ones, as well as the phenomenon of "emancipation of lower centers" from higher one's control if the latter are organically or functionally damaged (Kretschmer 1960; Vygotsky 1998, 83, 118-120, 219-222). The above principles formed an important motive not only for Vygotsky's

neuropsychology, but for genetic psychological methodology in general. As he observed, "the emancipation of lower centers finds a complete analogy in the emancipation of lower functions" (Vygotsky 1998, 123). Further, "the three basic patterns, observed in the development of the nervous system, specifically – preservation of lower centers in the form of separate stages [subordinate units], transition of functions upward, and emancipation of lower centers in pathology – conform perfectly to the history of development of mental functions" (Vygotsky 1998, 83).

Considering its well defined (physiological) features, the dominant may help to disclose respective genetic regularities and clarify their psychological role. Vygotsky repeatedly highlighted Bekhterev's genetic reflexological studies on the dominant, which seem of continued interest in this regard (Bekhterev & Shchelovanov 1969; Vygotsky 1997b, 153-177; Vygotsky 1998, 207-241). The experimental research of Bekhterev and colleagues pointed to dominants as laying the very base for forming new cortical associative connections in the child's brain, as well as determining the character and direction of these connections during early development (Bekhterev & Shchelovanov 1969). This confirmed Ukhtomsky's observations, according to which not only innate reflexes are subject to dominant-type alterations, but also conditional reflexes and higher psychological phenomena (such as associations, images, and recollection) (Ukhtomsky 1978). With regard to conditional learning, Bekhterev wrote:

> The establishment of new functional connections, i.e. the formation of associative reflexes is possible only when dominant processes of a general nature (attention) are present, occurring not only in the cerebral cortex, but simultaneously in lower segments of the nervous system [...] The time and order of forming the earliest conditional reflexes corresponds to the time and order of the development of the dominant (Bekhterev & Shchelovanov 1969, 25).

According to these materials, for an associative reflex to be formed, the receptive surface eliciting it must be capable of evoking a dominant functional affect and interaction in the nervous system. This interaction must be sufficiently widespread and consistent to inhibit and subordinate other functions and ongoing reactions. Thus, before the development of visual and aural dominants in the child, no conditioned reactions connected with their receptive areas can be formed. It was found that in the newborn, only feeding and position dominants are clearly established, and, correspondigly, the first conditioned associations can be formed only between these reactions (e.g., in the form of a feeding reaction arising when the child is placed in a position customary for feeding) (Bekhterev & Shchelovanov 1969; Vygotsky 1997b, 153-154; Vygotsky 1998, 222). At the beginning of the second six months of life, the formation of such reflexes begins to leave the sphere of the immediate influence of subcortical dominants (Vygotsky 1998: 222).[20] Most interesting here is the continued importance of attention and affect ("dominant processes of a general nature", in terms of Bekhterev), at first primitive and later in mediated forms, for establishing a common direction and scaffolding for sensory-motor processes (among which conditional associations represent but a special and derivative case)

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[20] It can be noted here that in the English version of this paper, a translation mistake has been made by stating that their formation "begins to enter the sphere of the direct influence of the subcortical dominants at this period" (see Vygotsky 1998: 222), thus effectively reversing the meaning of the original sentence.

(Vygotsky 1998: 207-241; Jantzen 2004). Here, Vygotsky's identification of the dominant as "nothing other than a physiological substrate of affect" seems significant, as both dominants and affects are presumed to underlie the unity of behavioral and experiential structures. This topic is more extensively discussed elsewhere (Jantzen 2004, 2005). We can here only highlight its clear parallel with modern views stressing the prime importance of emotions and affects for higher psychological functions in general (Schulkin 2014).

The relevance of the above observations on dominantogenesis seems thus not to be restricted to early developmental stages, where they indeed lend detail and confirmation to the genetic principles formulated by Kretschmer. The subsequent appearance in human development of voluntary behavior and conflicts between behavioral motives seems to recapitulate the problem of the dominant on a higher level: "In voluntary selection it is not stimuli that are in conflict, but reactive formations, whole systems of assemblies [...] The paradox of the will consists in that we create with its help an involuntarily acting mechanism" (Vygotsky 1997b, 213, 214). If the latter mechanism corresponds to a Pavlovian conditional reflex or automatism, then the process of establishing this type of involuntary mechanism proceeds quite differently both in psychological and neurological terms, and it needs to be analyzed first of all with respect to the person's motives (Vygotsky 1997b, 207-219). Through semiotic mediation, motives can create countless novel *closure mechanisms* or mobile physiological apparatus connecting sensory stimuli with efferent signals. Within such neoformations, the biologically "stronger stimulus may become the weaker motive and conversely, the stronger stimulation that automatically would have dominated the motor efferent path at the decisive moment would be breached [...] This stimulation can only affect the selection of the closure path tangentially, that is, only one-sidedly" (Vygotsky 1997b, 216). We can point here to the further elaboration of these ideas in Leontiev's theory of personality structure and motivation (Leontiev 2009a; cf. Bratus 2005; Jantzen 2009). Indeed, in the case of higher (cortical) dominants, it is possible to speak of their receptive surfaces only indirectly, as such dominants can be evoked by speech and thought signs, complex images of memory, traces from previous dominants, etc.

As a person learns to master cultural tools and semiotic devices, the structure of the psychological process in question can be controlled in a new way – its operations are modified not only internally, but first of all in their connections to other functions (Vygotsky 1997b). In this respect, the assumption that higher psychological functions correlate more closely among each other than with the corresponding forms of lower psychological functions (Vygotsky 1997b) is generally shared by current dual-process frameworks (Evans & Stanovich 2013). On the other hand, the position that higher brain functions therefore also depend on a qualitatively different (artificially, semiotically mediated) localizational principle in comparison to the brains of other animals and to non-mediated functions in the human brain seems no less interesting and relevant today than when it was first articulated by Vygotsky and Luria.

With respect to the problem of the dominant, we find Vygotsky's description of the effects of signs on higher forms of psychological processes similarly noteworthy. In his view, by thought and verbal instruction, dominant reactions can catalyze the effects of produced (speech) signs; thus they "intrude on the intercentral relations being created in the cortex of the brain, in the relations that play a decisive role in the control of our behavior" by sensitizing and catalyzing the appropriate nerve paths with additional, "artifical" stimulation. This view seems of particular interest, as around the same time (early 1930s), Ukhtomsky began to consider the

role of stimuli as catalytic triggers, excitatory states in terms of pulsating catalysis, and several years later, the respective oscillations in terms of their non-linear features, highlighting the potentially "disproportional" effect of ephemerally weak stimuli on the nervous system (Ukhtomsky 1978). This enabled him to elaborate on the earlier position, according to which the workings of a neural unit represent a function of its present condition: "Now we can state that this is a simple periphrasis of the claim that the neural unit is a non-linear oscillatory system" (Ukhtomsky 1978, 194). These important developments were unfortunately not available during Vygotsky's lifetime, as they drew on the theory of non-linear oscillations, the foundations of which were laid down in the mid-1930s. However, both the notions of catalysis (Cabell & Valsiner 2014) and non-linear dynamics (Dix 2014) are now increasingly evoked as important concepts for modeling living and cognitive systems behavior, and the modes of communication and systemic causation specific to them. The application of these concepts to understanding higher psychological functions remains, nonetheless, a largely unwritten chapter of psychology and physiology (but see Anderson et al 2012; Anastas et al 2014; Labra-Spröhnle 2016).

In light of the above, the maturation and formation of dominant constellations in the course of human development needs to be analyzed with respect to their culturally mediated structure and line of alteration. This problem was also pursued in the studies of the pedologist and psychiatrist Aron B. Zalkind (see Zalkind 2001), with whom Vygotsky was in close dialogue, in addition to Ukhtomsky's own humanistic legacy (first published only relatively recently; see Ukhtomsky 1996, 1997, 2001). This context makes it possible to speak of higher psychological and cortical dominants, including their chronogenic variation throughout life (Pavlova & Romanenko 1988; Pavlova 2016). Considering Bekhterev's and Vygotsky's detailed analyses of early biological dominantogenesis (Bekhterev & Shchelovanov 1969; Vygotsky 1997b, 1998), it seems that a better understanding of dominants could be significant for providing an integrative framework of basic science, encompassing the two highly bifurcated lines of biological and cultural development. With reference to P. K. Anokhin's works (1978, 1964), there have now been calls for a theory of the dominants' systemogenesis (Jantzen 2004), as a way to further extend systemic analyses of their biological maturation into adult life and culturally mediated forms.

Given all of the above, it is surprising that the relations between Ukhtomsky's and Vygotsky's thinking have attracted almost no attention, with a few rare exceptions (Jantzen 2004, 2005), and Ukhtomsky's legacy has remained virtually unknown in the West until recently (cf. Nadin 2015, 13-150). That the experimental study of 1926 remained the last empirical one by Vygotsky and colleagues on this topic may partially explain why it has not been pursued further regardless of its theoretical interest. Vygotsky's own premature demise, the ban on pedology, as well as the premature deaths of leading psychoneurologists investigating the dominant, Bekhterev (Bekhterev & Shchelovanov 1969; Lerner et al. 2005) and Zalkind (2001), terminated under tragic circumstances these most promising lines of developmental psychological and neurological research. The ideological climate of the period, increasingly under the sway of Pavlovianism, hardly favored even general physiological research on the topic, such as that carried out by Ukhtomsky himself and his followers (Sokolova 2015). As a result, these most original lines of research largely fell into disfavor and have remained little known since.

Unlike Vygotsky, his student Leontiev did not carry out specialized studies on the dominant. However, his psychological investigations are no less interesting with respect to its further development. As will be shown, Leontiev's studies enable an approach to dominants from the point of view of the macro- and microstructure of human activity in the course of practice and skill formation. This is the subject of the following sections.

7.4 Dominants of the Working Human Mind

7.4.1 Premises of Systemic Psychophysiological Study

As shown in the previous section, Ukhtomsky's principle of the dominant and Vygtosky's psychological studies confirm and substantiate each other on various levels. In both frameworks, the functions of a whole integral structure (dominant processes, behavior) were seen to be based on intricately differentiated and hierarchically organized dynamic relations in the systems of psychological and psychophysiological activity. Accordingly, higher coordinations not only influence lower ones, but can rearrange them qualitatively in the course of behavioral and psychological development.

The behavioral and psychological mechanisms of dominants can be further analyzed on the basis of Leontiev's theory of activity (Pavlova 1988, 2016). In this framework, Leontiev advanced the concept of the macrostructure of psychological activity entailing three basic links: motives, goal-oriented conscious actions, and operations (Leontiev 2009a). In his view, the dynamics of human activity and reorganization of its macro- and micro-structure – enlargement and division of action units, as well as transitions from exteriorized (externally unfolded) to interiorized (internally contracted) thought acts – are realized by the formation and reorganization of psychological and physiological "functional organs," pursuant to Ukhtomsky's description of dominants as functional constellations (Ukhtomsky 1978; Leontiev 2009a, 2009b). Accordingly, one of the main tasks of the psychophysiology of activity is to investigate the reorganization of dominant constellations in the course of macro- and micro-structural formation of psychological processes (Leontiev 2009a).

Both objective psychophysiological methods, such as EEG studies, and various behavioral measurements can be employed for this task. In Leontiev's own laboratory, tracking subjects' eye-movement activity in the course of experimental tasks was widely used as a method to investigate the micro-structure of psychological acts through behavioral measures. Parallel to this, EEG analysis provides a uniquely valuable source to disclose the rapid reorganizations of psychological and physiological processes occurring during task solution, practice, and mastery (Pavlova & Romanenko 1988; Pavlova 2000, 2016).

The above premises orient the study of all forms of activity to the time-course of their development and practice, which in the current framework has implied the gradual mastery of tasks over prolonged experimental trials (lasting 3-5 hours in a row) and repetitive tests until skill automatization achieves a pronounced form. Typically, we have investigated the same subjects in various test series and situations, often in the course of a number of years. These strategies respond to the requirement, often difficult to meet for technical reasons, of

investigating longitudinal changes in subjects' behavioral and cognitive control dynamics, as well as conducting their parallel psychological and psychophysiological assessment (Hoc and Alamberti 2007).

Going back to the 1960s (Sergeev et al. 1968), this approach has enabled the investigation and accumulation of detailed evidence on dynamic changes of test subjects' dominant cortical activation patterns in a variety of conditions, as well as the study of the effects of novelty and habituation with respect to any given type of cognitive process. The activities studied include a series of laboratory models of psychological activity, including externally embodied forms such as eye movement activity (EMA), as well as (corresponding) interiorized thought acts, in the course of solving various types of tasks (operator, verbal logical, spatial, heuristic, etc.).

In agreement with Leontiev, we consider only these types of studies to qualify as psychophysiological where changes in neurophysiological functioning are analyzed as resulting from the development of psychological processes and their structural modification.

7.4.2 The Dominant as a Model of Cortical Activation Patterns

The principle of the dominant introduces into cognitive science a factor which is rarely considered in other frameworks: non-equilibrium as a leading structural principle in all psychological and physiological processes. In line with Ukhtomsky's hypothesis on its organic bases, we elaborated in our previous works optimal statistical quantitative measures for characterizing functional shifts in the brain's dominant physiological state. This was identified by the momentary activation gradient between α- and higher frequency rhythms in accordance with Ukhtomksy's prediction (Sergeev et al. 1968; Pavlova & Romanenko 1988).

In this analysis (Pavlova & Romanenko 1988; Sergeev et al. 1968; Pavlova 2016), dominant brain states are reflected in two mutually exclusive EEG indexes that together characterize the magnitude of the dominant's non-equilibrium dynamics and localization: (1) the focus of heightened activity, reflected in the maximal desynchronization of α-rhythm (prevalent in the resting-state) and respective amplification of β- and higher frequency rhythms in a given region. These two factors define the the leading focus or the "*focus of maximal activation*" (FMA). (2) The subdominant regions under collateral inhibition, in which the uninterrupted and quasi-periodic α-rhythm is expressed maximally and reflects not only a state of physiological rest, but also an active functional blockage of task-irrelevant pathways (through collateral "pulsed inhibition" sent from from the leading activation focus, FMA) (cf. Jansen & Mazaheri 2010). This coupled inverse dynamics creates a non-equilibrium state, reflected in the magnitude of the *activation gradient* of a cortical activation pattern (cf. Pavlova 2015a; Pavlova and Romanenko 1988; Sergeev et al 1968).

Work on the basis of this model, as well as facts obtained by various analytical methods have led to one and the same conclusion: the EEG correlate of psychological states in cortical activity does not lie in individual frequency spectrums of the EEG, nor in the presence of correlations between them in any particular brain regions, but instead, in specific types of dominant cortical activation patterns (CAP) (Pavlova & Romanenko 1988; Pavlova 2000, 2015a, 2016) or dominant states of the "bio-potential field" as a whole (Fingelkurts and Fingelkurts 2010). We

have characterized this field by the structure of antero-posterior and inter-hemispheric activation gradients (AG). These methodological assumptions have been confirmed by more recent independent works (Koenig et al 2002; Fingelkurts and Fingelkurts 2010) and also agree with the systemic method as introduced previously, according to which the system as a whole needs to be described by integral tools.

7.4.3 Studies on human work dominants

Proceeding from the above theoretical background, this line of systemic studies has led to results that are in close agreement with current findings on the changing cognitive control strategies associated with practice and task mastery (Hoc & Alamberti 2007; Chein & Schroeder 2012), as well as with recent evidence on practice-related reorganizations in human brain activity (Kelly & Garavan 2005; Chein & Schroeder 2005, 2012). This is particularly notable, as most current evidence is obtained by alternative sources and methods (fMRI data).

Until recent years, the study of experience and practice related change in brain functions has been relatively scarce and mainly focused on changes in regional activity that accompany learning in particular task domains or control modalities (for reviews see Chein & Schneider 2012, 2005; Kelly & Garavan 2005). At the same time, the systemic nature of human learning and control processes is increasingly highlighted both in cognitive and neural studies of practice effects and skill acquisition (Chein & Schneider 2012; Hoc & Alamberti 2007). It is well known that cognitive and behavioral practice can lead to drastic changes in the accuracy, speed, and effort involved in almost any skilled action, either bodily or intellectual. Interpreting the observed functional activation changes in the brain will therefore necessarily depend on understanding the cognitive processes underlying task performance. Neural processes realizing cognitive functions can be expected to exhibit principled reorganization in case the performance of a highly trained, skilled, or automated action should depend on the (micro) development of a qualitatively different psychological process and structure, i.e., subjectively amount to solving a different task (Chein & Schneider 2012; Kelly & Garavan 2005).

These questions, addressed specifically in our research (Pavlova & Romanenko 1988; Pavlova 2016), may be particularly interesting in the context of historical and systemic approaches, where explanations of intra-individual and long-term performance variability represent a central theme (Molenaar 2008; Molenaar & Campbell 2009). These topics have remained largely ignored by standard approaches to time-series analyses, psychological experiments, and measurement (Molenaar 2008, Molenaar & Campbell 2009), as well as related cognitive neuroscientific frameworks (Cohen 2011), thus explaining the relatively recent interest, conflicting findings, and modest amount of systemic studies in the area of intra-individual variability and practice-related change (Chein & Schneider 2005; Kelly & Garavan 2005).

We present below a brief review of our approach and a summary model of its main findings, with particular reference to mastering human operator work tasks (Pavlova & Romanenko 1988; Pavlova 2016). As in all other experimental conditions, we have sought to maximally preserve the natural conditions of this activity in its experimental simulations and minimize

constraints on subjects' free movement. Natural conditions and forms of test activity make it possible to meet the criteria for sustaining high levels of meaning-making and motivation, which conduces to the formation of strongly dominant brain states and prolonged maintenance of active attention, as well as the establishment of necessary emotional tone in participants. At the same time, by solving tests and working over numerous trials, it has been possible to ensure the necessary standardization of tasks and possibility of quantitative (not only expert) assessment of work efficiency (Pavlova & Romanenko 1988; Pavlova 2000, 2016).

We are particularly interested in two aspects highlighted in the review of Hoc and Alamberti (2007), one more empirical and another of a more methodological nature. The authors note that one of the most pressing problems of cognitive psychology and ergonomics is to better comprehend and model the mechanisms of systemic dynamic inhibition of high-level (semiotically mediated) cognition in adjusting resource allocation and cognitive compromises, and more generally, regulating the cognitive cost of operations. The same question of structural inhibition could be crucial for understanding not only the processes of skill formation through resource optimization and automatization, but also transitions in the control strategy and modes of information processing (Pavlova and Romanenko 1988, Pavlova 2016), which remains a particularly difficult methodological challenge for current frameworks (Hoc & Alamberti 2007). In both cases, EEG investigations, due to their high temporal resolution, remain one of the most important analytical sources for addressing these questions. Psychophysiological analyses are indeed essential when the studied activities need precise qualifications and proceed in conditions of time deficit, have high requirements in terms of precision, selectivity, etc. (Leontiev 2009a).

Across diverse activities, we have found the phenomenon of α-rhythm "translocation" (Figure 7.2) between bilateral symmetrical and antero-posterior cortical zones to increase significantly in a state of intense mental and physical work load, corresponding both to CAP type reconfigurations and functional displacements within a given CAP type. Thus, the intensity of brain activity and work dominants is expressed not only in the magnitude of activation reaction (β-rhythm amplification and α-desynchronization), but also in the speed of cortical EEG "mosaics" transformation. Fast FMA translocations and CAP reconfigurations have been found to occur in all experimental settings and psychological states, and prove to be significantly more expressed between bilateral symmetrical zones (switching dominant FMA every 1-2 seconds, and faster) than in the antero-posterior direction, although these parameters show marked individual specificity.

This line of studies has led to the discovery of a highly reliable regularity in practice-induced changes in cognitive activity, termed by us the "coupled inversion" of antero-posterior and inter-hemispheric activation gradients (Pavlova 1979). We have interpreted this both in the light of Ukhtomsky's concept of the stage-wise formation of dominant reactions, as well as on the basis of Leontiev's and Vygotsky's work on the systemic bases of human activity. Together, these studies enable the elucidation of a general principle of chronogenic variation and reorganization of cognitive functions, a summary model of which is depicted in Figure 7.2.
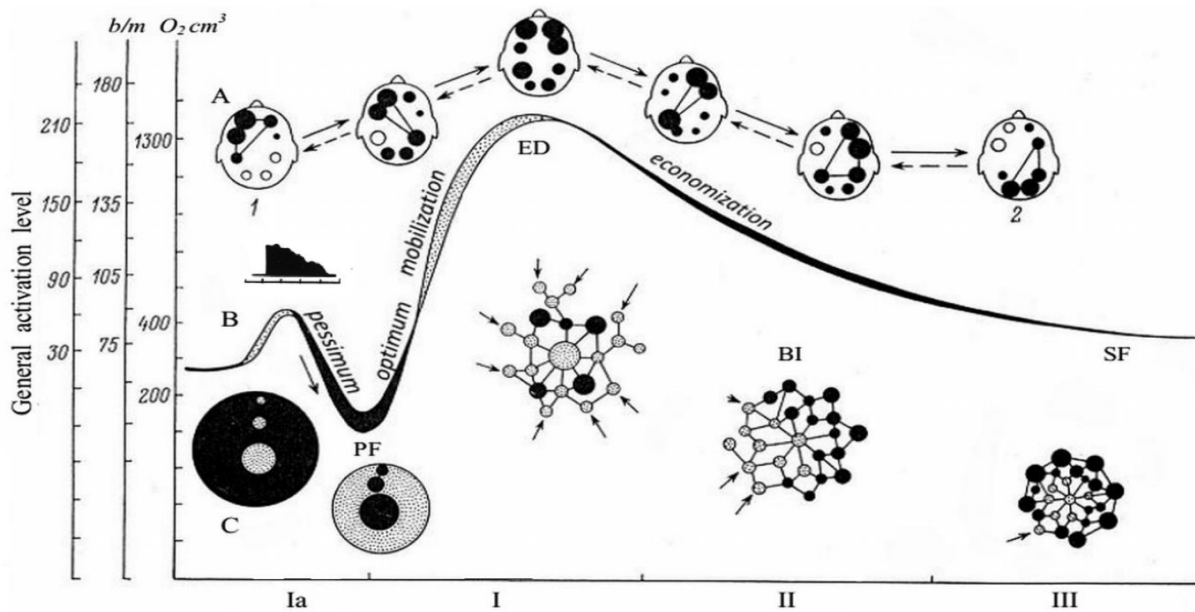
Figure 7.2. Process of active adaptation, or dominantogenesis (formation of working dominant). A—change of CAP types during transition from conscious goal-oriented actions (1) to automatized skills (2); solid arrows—process of adaptation, dashed ones—disadaptation; ED – expansion period of the dominant; B—graph reflecting the mobilization and economization of central nervous (general cortical activation level by EEG), vegetative (pulse, beats/min), and energetic (consumption of oxygen, O_2 cm^3) processes during consecutive stages of work/exercise (Ia, I, II, III); (C)—schematic representation of the state of neuronal ensembles according to Ukhtomsky (1978, 7-19, 63-90, 195-230): black color—regions of inhibition, white color—excitations; PF—primary fatigue; SF—secondary fatigue; in the second stage, arrows designate the reinforcement of the dominant ensemble by incoming stimuli during the ED period; BI— "barrier" of collateral inhibition during the automatization of the dominant (Pavlova & Romanenko 1988; Pavlova 2000).

During changes in the macro-structure of activity, such as transitions from purposefully oriented conscious acts to automatic operations (Leontiev 2009a), we have found that the dominant type of CAP would change in a highly predictable and regular manner across subjects and experimental settings. Independently of modality and the verbal/non-verbal specificity of the signal, novel situations requiring a new type of activity invoke the same type of CAP reorganization in all subjects, expressed in the translocation of FMA into frontal left cortical regions (Figure 7.2). This is graphically reflected in the coupled amplification of AG magnitudes between antero-posterior and bilateral symmetric zones. In the course of adaptation, the observed amplified activation of frontal and left-hemispheric neuronal mechanisms characteristic of novel situations is gradually replaced by another one, with increased activity in posterior and right-hemispheric regions. At the same time, a significant deactivation of left frontal cortical zones can be observed, above all Broca's speech and motor region (Figure 7.2).

We take this general pattern of gradient inversions to indicate a transition from the mainly sequential, linear, and verbally mediated type of information analysis that is typical for novel settings to a more automatic form of processing that requires significantly less involvement of conscious reflection and attention, and respectively the involvement of left frontal and pre-frontal zones. The latter are crucial for pre-mediated and intentional psychological acts

according to Luria (1980) and numerous recent studies. We observed this type of global reorganization or "coupled inversion" of activation gradients in diverse conditions of prolonged work and exercise: cyclic manual labor tasks, execution of complex movement stereotypes, one-dimensional visual and acoustic signal tracking, as well as complex intellectual activity while solving different types of psychological tests (of Eysenck, Wexler, and Raven), including those for verbal and non-verbal intellect (Sergeev et al. 1968; Pavlova 2000, 2016).

Our studies have confirmed a correlation between the level of adaptation and the frequency and extent of coupled AG inversion: FMA shows the highest stability in posterior right regions for habitual work operations which the subjects can execute in the absence of active attention (e.g., while entering a discussion with others). At the same time, while carrying out more complex types of activity – not only of the verbal-logical type, but also subjectively difficult ones involving concrete spatial tasks – the aforementioned right posterior FMA shift occurs only episodically and is statistically not notable on the background of frontal and left-ward activations. This has been shown in the study of individual dynamics as well as in group data (Pavlova & Romanenko 1988; Pavlova 2000, 2015a, 2016). Most interestingly, similar temporal gradients have also been descibed in evolutionary and developmental studies, where they seem to reflect chronogenic asymmetry along bilateral, antero-posterior and cortical-subcortical axes and activations (see Geodakyan V. A. 2005; Geodakyan S. V. 2015).

The works of Vygotsky's psychological school have shown that during the initial stages of mastering any psychological task the requiered activity assumes an extended, unfolded form: conscious attention is drawn to individual elements of activity, which are executed as purposefully oriented conscious actions (Leontiev 2009a). In the course of skill acquisition, by contrast, the activity undergoes a process of "contraction," as most of its elements disappear from the sphere of active attention and turn into unconscious automatic operations. During this latter stage active attention can be present only periodically. Corresponding to this, we observed momentary amplifications of left frontal FMA even on the background of highly automated acts. This would clearly reflect the transient "base points" of attention, in particular during the execution of signal tracking by operators (Pavlova 2000).

As indicated above, we see the presence of clearly defined FMAs as an expression of dominant foci as understood by Ukhtomsky. These are characterized by heightened excitability, ability of excitation summation, as well as excitation re-routing and inertia. By these means, FMAs and their translocations can determine the direction of behavioral manifestations and subjects' variable reactions towards externally similar and identical situations, as well as underlie the changing psychological and neurological basis for realizing externally similar or identical behaviors. Regardless of external similarity, activities can have psychologically and physiologically different internal structure both across individuals and within the same individual over time. This makes chronogenic, i.e., developmental and intra-personal analyses inevitable parts of human cognitive science.

One of the most robust patterns found in current practice-effects literature (Kelly & Garavan 2005; Chein & Schneider 2005, 2012) confirms the increased activity of higher-order metacontrol mechanisms and (anterior) associative regions during initial stages of practice. Over the course of adaptation these areas show reliable decreases in activity, paralleled by increased involvement of lower-order sensory (posterior) areas (cf. Figure 1 in Chein & Schneider 2012). This confirms our findings and the principle of "coupled inversion" of AGs,

obtained through alternative methods across various conditions (Pavlova & Romanenko 1988). According to these findings, the development of highly dominant CAPs of cognitive and physical work follows a chronogenic stage-wise structure, reflecting Ukhtomsky's conception of the dominants' formation through consecutive phases of excitation generalization and concentration, in line with activity maximization and minimization in the course of practice, respectively (Ukhtomsky 1978: 7-19, 63-90, 195-230). This model has made it possible to generalize the above observed practice-related dynamics to analyze overall activity patterns in the organism, involving not only patterns of psychological and central nervous activity, but also shifts in peripheral activation in the course of adaptation (Figure 7.2). This process of adaptive functional reorganization has been termed dominantogenesis (Pavlova & Romanenko 1988; Pavlova 2000).

The above results underscore the fact that the psychophysiological problem is not restricted to general psychological aspects, but needs to be resolved simultaneously, if not primarily, in the individually variable aspects of higher psychological functions and their realization in the brain (Pavlova 2015b). This represents a central feature of the systemic approach as developed here. Dominant states with a clearly expressed FMA do not arise simply as a result of information entering the central nervous system and stimulating certain cortical regions. A decisive role in the formation of brain dominants is also played by the motivational and emotional sphere of the personality, the psychological set of the individual (Uznadze 1966). As Hoc and Alamberti stress (2007), it is often the inner competitive and continuous focus on individual (emotional and personal) affairs that seems to explain bizarre arbitrations in performance, although – in comparison to more objective situational requirements and subject's expertise – information pertaining to the emotional state and wider cognitive focus of the subject has been insufficiently considered in current studies and calls for new, more complex and individual approaches (Hoc and Alamberti 2007). In our works, we have proceeded from the concept of two complementary factors in the formation of CAPs. These are expressed (1) in the specifics of CAPs that are adequate to the performed activity (its preconditions and circumstances); and (2) CAP features that are characteristic for a given individual in a particular state.

These two factors can coincide to various degrees, as well as change in the course of activity. In the latter case, this change defines the speed of professional adaptation. According to our findings, the degree of adaptation corresponds to the degree of adequate CAP reconfiguration with respect to the anticipated activity already in the preparatory stage, i.e., the state of psychophysiological rest. On the other hand, the correspondence of CAP type to the class of required work is determined during the later, adaptation stage, although here also individual activity features are preserved in the CAPs of various subjects. Overall, we have studied the dependence of work productivity on initial individual CAP type in more than 500 subjects in various experimental conditions (Pavlova 2000; Janvaryeva et al. 2001).

The conclusion that CAPs correspond to units and individual patterns of mental activity is further confirmed by special studies on the micro-structure of operator work, where the dynamic organization of EEG has been superimposed with phases of test subjects' eye movement activity (EMA) while they solve dispatching tasks. These experiments have particular interest from the theoretical perspective outlined above regarding the parallel operation and possibility of fast reversions between distinct cognitive control modes, as well as in connection with the

problem of voluntary inhibition of meta-cognitive (symbolic) planning and intervention (Hoc and Alamberti 2007). Respective experiments required visuo-logical search activity in order to quickly find the shortest and safest route between two points on a schema (1×1.5 m) according to task conditions. This requires intense visual concentration while perceiving large amounts of information in conditions of time deficit (Figure 7.3). Solution efficiency (speed and accuracy) was found to correlate most clearly with increased general activation, presence of high AGs in the initial resting state and while solving the task, as well as with the translocation of FMA into right frontal zones in periods of saccadic motion. Most interestingly, and obligatorily for a successful solution, during fixation pause periods, a specific type of CAP had to be formed, which we have observed to correspond to the moment when the subject finds a heuristic solution method (seen also in other similar experiments). This type of CAP (at t_3 in Figure 7.3) is characterized by a "crossed" localization of FMA simultaneously in right frontal regions and the left posterior speech zone of Wernicke . During the fixation pause left frontal zones are significantly deactivated, particularly the speech-motor region of Broca, reflecting an inhibition of discursive thought (reflection, internal speech) in the periods corresponding to the "detachment" of the image from its concrete surroundings after it has been detected and represented during the first phase of saccadic motions, according to Zinchenko's schema (Zinchenko & Vergiles 1995). This deactivation of speech zones seems to indicate the difficulty in apprehending and becoming aware of the thought acts occurring on the internal plane, particularly during intuitive acts. In the case of successful solutions, an activation increase of Broca's area was observed in the first period of saccadic motion while becoming familiar with the task. After that, however, during the formation of the perceptual image (at t_2 in Figure 7.3), the same area is deactivated simultaneously with the posterior speech region of Wernicke on the background of significant amplification of prefrontal and visual zone activity. This type of CAP (with both speech areas blocked) can be observed in various types of operator activity in conditions of time deficit, and it seems to correspond to an externally unfolded thought act which, judging by the right-ward asymmetry, is primarily based on non-verbal spatial-temporal perceptual codes and analysis. In the current example, during the final stage of saccadic activity (after which the correct answer was given, 4-5 seconds from task onset), increased activation of the frontal speech regions can again be observed, which seems to indicate a reflexive process of reconstructing the image consciously in line with the solved task. While the duration of successful solutions did not exceed 4-5 seconds, it is telling that in unsuccessful or too slow solutions (16–30 seconds and above) the "heuristic" CAP type could not be seen and the sequence of CAP transitions discussed above was not present in the test subjects.
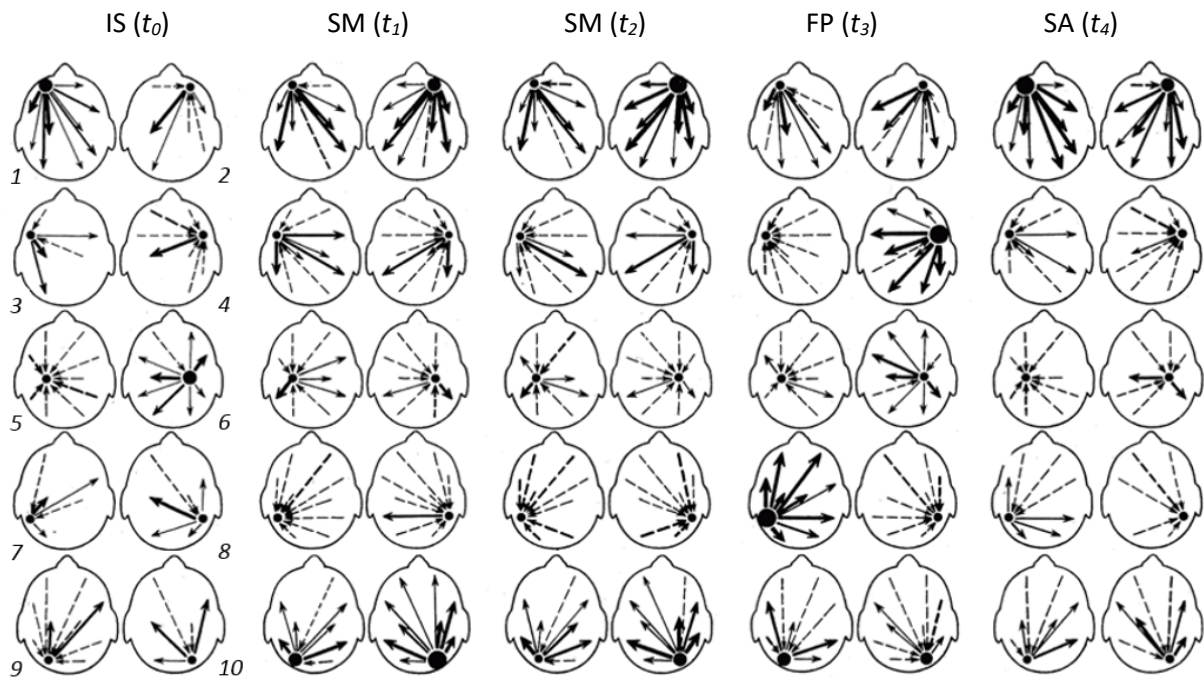
Figure 7.3. CAP type dynamics in the course of successfully solving a dispatching task, mapped to successive phases of eye-movement activity. IS (t_0)—initial state; SM (t_1, t_2)—periods of saccadic motion (examination of the field of activity); FP (t_3) fixation pause (guessing a solution); SA (t_4)—average saccadic activity (realization of ideas, execution of actions). The width of solid lines on hemispheric projections designates FMA activation gradients (the "source" regions) with respect to other cortical regions. Deactivation magnitudes (in "sink" regions) are designated by the width of hatched arrows. Numbers indicate symmetrical recorded regions: 1, 2 anterior-frontal (left and right); 3, 4 frontal temporal areas – speech zone of Broca (left) and symmetrical (right) one; 5, 6 parietal areas (left and right); 7, 8 temporo-parietal areas – semantic zone of Wernicke (left) and symmetrical (right) one; 9, 10 – occipital (left and right) regions. Activation gradients calculated by K beta/alpha.

While comparing repetitive solutions by the same test subject, entirely stereotypical sequences of EMA and CAP cannot be found, and a significant individual diversity of CAP types is present during all phases of EMA, along with the clear influence of the initial CAP state which extends throughout the EMA phases. This indicates individual diversity in the neurological realization of similar psychological states, and also a lack of clear neuronal templates for psychological acts intra-individually. However, the individually habitual type of CAP correlates strongly with the efficiency of task solution, and underscores the notion of optimal neuronal regimes with respect to a given type of psychological activity, i.e., the optimal ability to reconfigure the dominant CAP type in view of the task requirements and its consecutive stages.

7.5   Conclusion

The results summarized above testify to the fundamental role of psychological concepts and models for understanding human higher brain functions. To understand the mechanisms of human psychological and psychophysiological processes in their social formation, it is

necessary to see that this influence is mediated by activity. In other words, the restructuring and reorganization of psychological and psychophysiological functions and mechanisms is led by the necessity of modifying adaptive processes and forms of human macrostructural behavior. Although a more detailed presentation of the results and methods of these studies is not possible here, we hope to have indicated their relevance for the systemic study of practice related psychological and neurophysiological reorganization in the context of modern research. This constitutes a specific application Vygotsky's principle, according to which the localization of higher psychological functions can be understood only from a chronogenic perspective. Accordingly, the systemic dynamic principle of analyzing and localizing psychological processes needs to be understood not only in relation to the ontogenesis of cognitive and brain functions, but also with respect to the active behavioral formation of working dominants as functional systems of the mind over the whole course of human life.

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STUDY 3.

Pavlova, L. P., Berlov, D. N., & **Kurismaa, A.** (2018). Dominant and opponent relations in cortical function: An EEG study of exam performance and stress. *AIMS Neuroscience*, 5(1): 32-55.

Author contribution:
The author conceived the idea and drafted the paper. L.P. Pavlova provided materials from her original studies (sections 3–4), which were included into the text with the help of her colleague D.N. Berlov.

Theory article

Dominant and opponent relations in cortical function: An EEG study of exam performance and stress

Lucia P. Pavlova[1], Dmitrii N. Berlov[2,3] and Andres Kurismaa[4,*]

[1] Department of Higher Nervous Activity and Psychophysiology, Faculty of Biology, St. Petersburg State University, St.-Petersburg, Russia

[2] Department of Anatomy and Physiology of Humans and Animals, Herzen State Pedagogical University of Russia, St.-Petersburg, Russia

[3] International Research Center of the Functional Materials and Devices of Optoelectronics and Electronics, ITMO University, Saint Petersburg, Russia

[4] Department of History and Philosophy of Science, Faculty of Science, Charles University in Prague, Czech Republic

* Correspondence: Email: andres.kurismaa@gmail.com; Tel: +420776039262.

Abstract: This paper analyzes the opponent dynamics of human motivational and affective processes, as conceptualized by RS Solomon, from the position of AA Ukhtomsky's neurophysiological principle of the dominant and its applications in the field of human electroencephalographic analysis. As an experimental model, we investigate the dynamics of cortical activity in students submitting university final course oral examinations in naturalistic settings, and show that successful performance in these settings depends on the presence of specific types of cortical activation patterns, involving high indices of left-hemispheric and frontal cortical dominance, whereas the lack thereof predicts poor performance on the task, and seems to be associated with difficulties in the executive regulation of cognitive (intellectual) and motivational processes in these highly demanding and stressful conditions. Based on such knowledge, improved educational and therapeutic interventions can be suggested which take into account individual variability in the neurocognitive mechanisms underlying adaptation to motivationally and intellectually challenging, stressful tasks, such as oral university exams. Some implications of this research for opponent-process theory and its closer integration into current neuroscience research on acquired motivations are discussed.

Keywords: cortical activity; dominant principle; electroencephalogram; functional asymmetry; individual variability; opponent processes

1. Introduction

In the current paper, we focus on two basic, interrelated principles of systemic regulation of brain functions—the opponent process theory by R.S. Solomon [1–3], and A.A. Ukhtomsky's principle of the dominant [4,5], and apply them to electroencephalographic (EEG) analysis of human performance at university oral exams in naturalistic conditions [6]. By drawing on the experimental results of this pilot study, we demonstrate that successful adaptation of students to the requirements of an oral examination depends on the presence of individual types of cortical activation patterns (CAPs), involving high indices of left-hemispheric and frontal cortical dominance, whereas the lack thereof reliably predicts low achievement on the task, and seems to be associated with difficulties in the executive regulation of cognitive (intellectual) and acquired motivational processes in these highly challenging and stressful conditions. Findings from these studies seem to support several key tenets of Solomon's opponent process theory of motivation dynamics [3], and may help to analyze its so far relatively poorly understood neurophysiological mechanisms in the light of the dominant principle [4,5]. In particular, the widely prevalent, if not universal functional principle of coupled opposed dynamics (COD) of cortical activity, as revealed in the principle of the dominant, can be of fundamental importance for elucidating how functional cerebral systems with mutually exclusive and opposed effects interact in time, leading to both adaptive or maladaptive behavioral and cognitive responses. We introduce functional measures of COD, such as the coupled inversion of anterio-posterior (fronto-occipital) and bilateral (inter-hemispheric) activation gradients, to analyze these responses, and show how their dynamics change in different task conditions and cognitive states in a manner consistent with the opponent process theory.

Methodologically, analyzing the neurophysiological dynamics of motivational reactions in ecological settings may require specific approaches, and this has been rarely attempted in exam conditions. While numerous works are devoted to the role of emotions, stress and anxiety in the learning process [7–9], including the exam situation, virtually all such studies are limited to pre-examination and post-examination analysis [10–15], without affecting the exam itself, particularly with regard to measuring the brain's bioelectric activity in the course of the exam interaction and presumable peak stress experience. The current line of studies sought to validate the applicability of dynamic EEG analysis in these settings [6,16,17]. It may therefore represent particular interest for analysing not only the electrophysiological correlates of opponent processes, as understood by Solomon, but also for considering their so far little explored social and interpersonal aspects in relevant natural settings.

As will be shown, based on such knowledge, the individual variability of dominant and opponent processes can be analyzed, and improved pedagogical and therapeutic interventions suggested which take into account marked individual differences in the neural and cognitive mechanisms underlying adaptation to motivationally and intellectually challenging tasks, such as the oral exam. These aspects will be more extensively addressed in the discussion, after the concepts of the dominant and opponent processes have been introduced (section 2), and relevant empirical materials presented (section 3). Theoretically, the integrative approach developed here [6,16,17] corresponds to the widely recognized need for systemic frameworks and methodologies in the fields of behavioral and human neuroscience [18,19], and in the analysis of EEG [20,21], in particular.

2. Dominant and opponent processes

In the fields of neuroscience and psychophysiology, both the theory of opponent processes, as well as the principle of the dominant stand out by their systemic, heuristic predictions and specific applications in an unusually wide range of topics. Thus, Solomon and Corbit [1] proposed a general model of opponent processes to explain an apparently widespread mechanism securing the dynamic homeostasis of intense, contrastive emotional and motivational states [3]. The authors gathered evidence from physiology and psychology for a general model explaining how intense hedonic experiences can automatically induce in the nervous system a biphasic, compensatory motivational or affective process of opposite hedonic valence, before a return to stable affective baseline state occurs in the subject. However, the neurophysiological underpinnings of this dynamic homeostatic phenomenon have remained relatively elusive and little studied, in comparison to its behavioral and psychological effects.

Recently, some of the related methodical and methodological challenges have been discussed by Comer et al. [22]. In particular, the authors propose that the functional cerebral systems theory of A.R. Luria [23] may still provide "unsurpassed explanatory value and testability" in promoting the systemic-dynamic exploration of functional processes within the nervous system [22], including the relevant homeostatic and compensatory effects. Indeed, such aspects have remained largely underappreciated, and challenge current attempts to integrate opponent processes into mainstream neuroscience research, according to their view [22].

Here, we suggest that besides the works of A.R. Luria, valuable insights for the study of dynamic functional systems can be obtained from a historically and methodologically closely related tradition, namely A.A. Ukhtomsky's study on the dominant [4,5]. The fundamental basis informing this line of work concerns the unity of opposed functional processes in the brain—excitation and inhibition—as tonic neurophysiological states, and their reciprocal induction in cortical and neuronal excitability [24–26]. In particular, this approach may help to understand how intense work-load on any functional system—of immediate hedonic valence or not—can evoke its auto-inhibition and resultant "super-compensatory" effects, before a more stable baseline of excitability is restored or modified in the brain. In the present paper, we are limited to discussing this phenomenon in its cortical physiological aspects.[21]

The dominant approach allows to highlight how the opponent temporal dynamics of motivations and emotions may depend on the non-equilibrium properties of the cortical

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[21]Currently, the concept of *hormesis* is widely discussed as a general biological model of state-dependent functional effects in physiological systems, particularly in relation to the varying and opposed effects which neurotransmitters and other substances may have at the cellular level, depending on their concentration (dose-response effects) or other conditions of exposure [77]. On the other hand, the conceptual and historical parallels of the hormetic research paradigm with the framework of parabiosis and paranecrosis, going back to Ukhtomsky's teacher N.E. Wedensky's and D.N. Nasonov's works [78,79], are also recognized [80,81]. These aspects lay beyond the scope of this paper, but are important to theoretically highlight, particularly given the recent interest in hormetic phenomena in the nervous system [82,83]. Without addressing such opposed phased functional effects, it may be difficult to develop a low-level neuronal interpretation of opponent processes in relation to particular transmitter systems, as currently sought [84,85], and thus firmly ground opponent process theory in biology. Interestingly, the school of Wedensky-Ukhtomsky appears to remain the only physiological tradition where principles characterizing homeostatic phenomena at the neuronal level, and the functional state parameters of general, brain-wide dynamics have been investigated from a common perspective [25,86].

biopotential field as a whole. This field can be characterized by transitions in the *foci of maximal activation* (FMA), and by the localization of the accompanying coupled, collaterally inhibited areas in the surrounding cortical tissue. These two contrastive neurophysiological responses represent a pattern of *coupled opposed dynamics* (COD) in the cortex that seems to be of wide, perhaps universal relevance for interpreting neurophysiological coordination dynamics and mechanisms [6,17,27] (section 3).

In particular, this approach to opponent processes may allow to better understand the mechanisms governing dynamic changes in hemispheric dominance [22,28], as well as to demonstrate how shifts in inter-hemispheric and prefrontal dominance relate to changes in the motivational and higher cognitive processes of subjects as they adapt to diverse task conditions and cognitive work load [6,16,27]. Below, we show evidence for the hypothesis that opponent motivational processes may be directly related to changes in hemispheric and prefrontal dominance indices. While this hypothesis has been proposed and is supported by other experimental paradigms and evidence [22,28], the current approach allows to extend and generalize these findings by applying a novel experimental and methodological framework for their neurophysiologically rigorous and ecologically valid investigation—albeit in a small-scale pilot study.

It can be noted that respective materials raise also general theoretical problems, as they highlight that shifts in motivational states are most probably not limited to the sphere of "hedonic" processes or specific subcortical regions in the brain, but seem to involve widely distributed functional cerebral systems, including cortical ones associated with higher psychological processes and executive functions in humans. Although direct EEG evidence on opponent effects is so far limited, a recent study by Kline et al. [28] has obtained relevant results in this regard and should be shortly highlighted.

The authors revealed the role of prefrontal cortical regions in the opponent-type regulation of emotional experience, and showed how the organization of this experience depends on the dynamics of hemispheric functional asymmetry. In particular, it was shown that fear reactions evoked in a group of participants (in response to aversive pictures of human faces) are accompanied by increased relative right prefrontal activation, whereas the predominance of left prefrontal regions inhibits the same negative reaction and may, in well-coping subjects, respectively show enhanced and super-compensatory activity after the initial fear response. The authors interpret this increased leftward activation as a contrastive after-reaction necessary for suppressing, on an opponent process basis, the mainly right-hemispheric aversive response [28]. Although not obtained in an exam setting, these results seem to confirm the view that opponent affective processes, as conceived by Solomon, are closely associated with a corresponding contrastive dynamics in frontal lobe activity. A replication of this hypothesis in other experimental paradigms would be highly desirable, nevertheless, to demonstrate the pervasiveness of such opponent regulations and their possible functional contexts. This could also lead to a better understanding of the intra- and inter-individual variability which such opponent effects may have, their task-specificity, as well as association with other neural systems.

Close to the present focus, an early study by Craig and Siegel [29] has addressed the principle of opponent regulation in the exam situation. The authors investigated habituation to test-anxiety in college students and obtained evidence supporting Solomon's theory. In particular, by administering mood adjective checklists to students for self-rating just before and immediately after taking a final course exam, the authors quite expectably found a reliable

decrease in dysphoria—but more significantly, also an increase in euphoria subsequent to the stressful test event, consistent with the opponent process model [29]. The important implication of the latter is the prediction of not simply attenuating apprehension, but also a surge in elation upon completing the exam. However, this study did not employ any physiological measures, and together with other related studies on exams [10–12,30], would clearly benefit from an integrated psychophysiological approach, allowing to analyze the neural substrates and mechanisms directly involved in the exam situation and interactions [16,17]. Likewise, most research on emotional and stress reactions has so far investigated EEG and peripheral signals separately [31], although their fusion and joint assessment may improve the robustness of both lines of findings [31], as our own data in the exam setting also suggests.

As shown below, our research on the higher cortical regulation of cognitive and motivational processes are in direct agreement with the above results [28,29], and may help to generalize and extend these findings on opponent-type regulation to more complex types of motivational and cognitive responses—such as involved in real-time exam situations. Before turning to the empirical findings obtained in this framework, we will briefly describe some methodological specifics of this line of studies based on A.A. Ukhtomsky's principle of the dominant. Further integration of this approach and findings with opponent-type processes is presented in the discussion.

3.   Theoretical preliminaries: The dominant and human EEG

It's passing first to consider A.A. Ukhtomsky's pioneering insights on the functional role of EEG rhythms. Based on the concept of "operative rest" or calm (cf. [32,25]), his views were among the first to clarify the controversial issue of the quasi-periodic alpha-rhythm (8–10 Hz) and its significance in human brain activity. Ukhtomsky proceeded from the experimental fact that in humans, the resting state is dominated by coherent, low-frequency alpha-waves of high amplitude. Peripheral stimuli from sense organs are known to disturb this "resting-state oscillation" and to give rise to higher-frequency activation (beta rhythms > 12 Hz) in the cortical projections, further enhanced by the subject's endogenous attentional and emotional arousal. These facts led Ukhtomsky to conclude that it would be *incorrect to see coordination as being generally based on the synchronization of neuronal activity alone* [4]—more often than not, *it depends on a parallel increase in the desynchronization of neural networks* [4,6]. This constitutes a general principle of *coupled opposed dynamics* (COD) in brain function, as clarified below.

Elucidating the role and mechanisms of alpha-rhythm desynchronization continues to be an active area of research, where various general and more specific hypotheses have been offered to account for its functions. Jensen et al. [33] have framed an influential view on the gating and filtering properties of the cortical alpha, which through targeted suppression (" pulsed inhibition") of higher-frequency rhythms, particularly gamma oscillations (30–70 Hz), is assumed to have an active inhibitory role in shaping functional cortical architecture. Closely compatible interpretations have been recently proposed by Klimesch [34], who suggests an active inhibitory function for alpha activity in controlling attentional and conscious access to stored memory and knowledge; for this access to occur, information from competing sources must be temporarily excluded (suppressed). In more formal terms stemming from information theory, alpha desynchronization can be related to information richness in the brain, necessary for the encoding and retrieval of memory and other cognitive processes [35]; on the other hand, the degree of synchrony in neural firing patterns is inversely related to their information

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carrying capacity [35]. Indeed, hypersynchronized cortical activity in the alpha range has been associated with complete blockage of intracortical communication, leading to the breakdown in sensory processing and loss of consciousness [36]. Important studies, closely related to our own, have also been carried out in the framework of coupled event-related desynchornization/synchronization (ERD/ERS) by Pfurtscheller and colleagues, suggesting that cortical activation (reflected in ERD) may be more focused and concentrated when surrounded by fields of antagonistic inhibitory synchronization (ERS), particularly within the alpha band [37–39].

Thus, modern studies seem to offer numerous confirmations regarding the dominant concept and its application in the field of EEG study. At the same time, some methodological differences regarding the principles of EEG analysis should be noted. This concerns above all the problem of dynamic features of neural signals, specifically the non-stationary (discontinuous, segmentary) and stochastic properties they exhibit. While knowledge of such features has been available for a long time (and forms the basis of our work [40]), they have typically been ignored in current and classical frameworks of EEG interpretation due to methodical and theoretical premises [20,21]. On the other hand, while this may simplify signal analysis, neglecting such dynamic features has also lead to significant difficulties in constructing global models of the EEG phenomenon, and in relating it to problems of cognition and consciousness [20,21]. Thus, novel methodologies sensitive to the underlining quasi-stationary nature of the EEG signal are clearly necessary [21]. One of the earliest such frameworks has been developed in collaboration with one of the authors (L.P.) [17,40] on the basis of the dominant principle. Below, some of its key premises and methods are briefly outlined.

The principle of dominant introduces into cognitive science a factor rarely considered in other frameworks—the factor of non-equilibrium as an invariant principle in all neurocognitive phenomena. In its most general form, Ukhtomsky characterized dominant states as consisting of two coupled and inverse processes—a leading "focus" or excitatory link, and systemic propagation of inhibition over the remaining elements of the system. This divergent pattern constitutes a universal mechanism of coordination in his view, and the means by which superfluous degrees of freedom are eliminated in neural systems. In this context, dominance is not so much a theory or hypothesis, but an obvious feature of functional cerebral systems in his view. However, it can offer powerful heuristics for studying brain activity when constrained by specific models and analytic methods, and may prove to be its highly universal organizational feature.

It is thus instrumental to define an adequate model for dominant states and the associated non-equilibrium dynamics in brain networks. The dominance model outlined below presents methods for multi-parametric and multi-channel analysis of such functional dynamics according to coherence and synchrony parameters [6,40]. Accordingly, the activation gradients (AG) characterizing functional asymmetry indices along anterio-posterior (AP) and bilateral (LR) interhemispheric cortical zones define the structure of cortical activation patterns (CAPs), and their "non-equilibrium" (functional asymmetry). In our previous works, we elaborated optimal statistical quantitative measures for characterizing functional shifts in the brain's dominant CAP states, defined by the momentary activation gradients between α- and higher frequency rhythms [40,17] (Appendix 1).

In this model, a dominant CAP state is reflected in two coupled inverse shifts in regional biorhythm indices characterizing cortical areas: (1) a focus of maximal activation (FMA), with

amplified β-rhythms in a given region and attenuated α-oscillations (down to their complete disappearance in that area); and (2) a state of coupled inhibition in the surrounding cortical regions, as reflected in the simultaneous appearance of amplified α- rhythm [6,17] (Appendix 1).

Additionally, an activation coefficient $K_{C/O}$ can be determined by the relation of latent reaction periods (LRP) after closing and opening the eyes—with LRP for closed eyes (LRP–CE) reflecting excitation inertia, and LRP for opened eyes (LRP–OE) reflecting inhibition inertia, or the inertial properties of inhibitory cortical states (Appendix 2).

4. Experimental studies on exam performance

Oral exams present one of the most intense forms of human mental activity, combining both intellectual, emotional, and stress-regulatory components in a highly dynamic social setting [6]. Examining their individual variability and neurocognitive structure may therefore present unique insights into the mechanisms of opponent processes in naturalistic conditions.

4.1. Methods and materials

Our studies were carried out in an experimental EEG recording facility in collaboration with Dr. N. Volkind from Krasnoyarsk Pedagogical Institute, with whom we conducted university term examinations on the subject "physiology of higher nervous activity" on volunteering student participants from St.-Petersburg State University's Psychology Faculty. To ensure high performance criteria, students' examination grades were recorded on exam sheets and reflected in their official study records.

Experimental conditions: In a group of 20 students (18 y.o., male, all right-handed), EEG was recorded continuously from 8 to 10 symmetrical anterior and posterior cortical sites (using the device "Biofizpribor", 0.3–100 Hz bandwidth), simultaneously with electrocardiogram (ECG) data [6,17]. Electrode montage is specified in Appendix 3. On the eve of the exams, a test experiment was carried out on each participant to ensure habituation to exam settings and to the Eyes Closed/Eyes Open (EC/EO) test (Appendix 2). Each experimental session lasted for no less than 1.5 hours in a row, during daytime, under normal daylight conditions. EEG recordings were made as the subjects were seated in a comfortable chair, in a specially screened room (3×3 m^2) shielded from external noise. After installing the electrodes, the FAM test (Feeling, Activity, Mood) [41,42] was administered to students, who thereafter were left alone for 15 minutes to rest and prepare before starting the exam. After completing the exam, students were left to rest for 20 minutes, before being again administered a FAM test by the experimenter. Furthermore, prior to the experiment we tested subjects by the Hand [43], personal orientation inventory (POI), and Eysenck personality questionnaire (EPQ) psychological tests.

Students' EEG and ECG were recorded continuously throughout 5 stages of the exam: I stage—students await for the examiner, corresponding to a state of operative rest (15 min); II stage—the examiner enters the room, students receive tickets (topics), read them in the examiner's presence, the examiner leaves; III stage—students prepare independently an answer to the ticket (20 min); IV stage—students are orally examined on the ticket and on additional questions, are notified of their grade (20 min); V stage—period of post-exam rest, the examiner has left (20 min). Throughout the whole exam, short EC/EO tests were administered every 2–3 min.

It should be stressed that we did not assess FAM scores by averaging results across the participants, but distinguished between 2 experimental subgroups by their grades—a high-achieving group (A), who passed for "excellent", and a low-achieving group (B), who either failed the exam or passed it poorly. This strategy was used to reveal adequate correlations between CAP types and given sets of activity. While selecting students to be included in either group by their grade, we strove to maintain their homogeneity also by other indices, above all by high achievement motivation, which was present in all subjects. (In group A, all 5 students had "excellent" academic records exclusively in all subjects, and had all graduated with honors from highschool. In group B, students with high achievement motivation and generally good knowledge of the subject were chosen, but who failed to demonstrate this knowledge in the specific settings of an oral exam, both in the current study and during prior oral exams). These inclusion criteria were applied meticulously, particularly given the small sample size of the study.

Ethical conditions: The study was conducted on unpaid volunteers. Experimental procedures of study, including its ethical and medical aspects, were reviewed and approved by an expert committee at the A.A. Ukhtomsky Physiological Research Institute at St.-Petersburg State University. Participation in the study involved written consent from students and Deans of the Psychology and the Biology Faculties of the University.

4.2. Results

Most significant shifts in the level of cortical activation (by the coefficient $K_{C/O}$) (Appendix 2) and vegetative nervous activity (pulse rate) were observed in stages II and IV of the exam—while drawing the ticket and answering it, respectively. Signs of examination stress were particularly pronounced in highly anxious, poorly answering students (Figure 1).
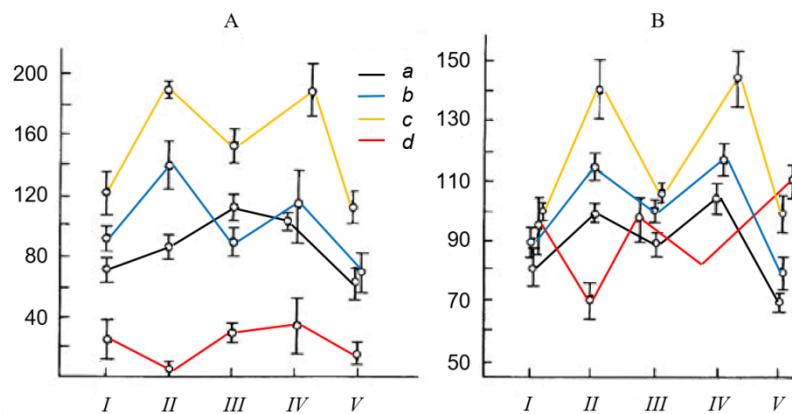

Figure 1. Shifts in general activation of cerebral cortex (A) and pulse rate (B) in consecutive stages (I–V) of oral examination in four variously graded groups (5 subjects in each group). *Ordinate*: A—average measures of general cortical activation ($\Sigma K_{C/O}$, in conditional units), B—pulse rate (bpm); *a, b, c, d*—grades received: excellent *(a)*, good *(b)*, average *(c)*, poor *(d)*, respectively. Abscissa—exam stages: *I*—waiting; *II*—drawing a ticket; *III*—preparing the answer; *VI*—exam response; *V*—after-effects.

Significant individual differences in the indices of general cortical activation by $K_{C/O}$ (Figure 1A) and pulse rate (Figure 1B) can be seen in relation to success rate at the exam.

During all stages of the exam, students receiving excellent and good grades (groups a and b) showed intermediate values for these indices, in comparison to students receiving average and poor grades (groups c and d). Thus, less successful responders where characterized either by an excessive degree of cortical activation and pulse rate (group c), or an insufficient value of these functional indices (group d), in comparison to the high-achiving groups. The reliability of this data is increased by the identical conditions in which all examinees were tested, and the highly significant differences in functional brain states of high- and low-achieving participants (Figure 2).
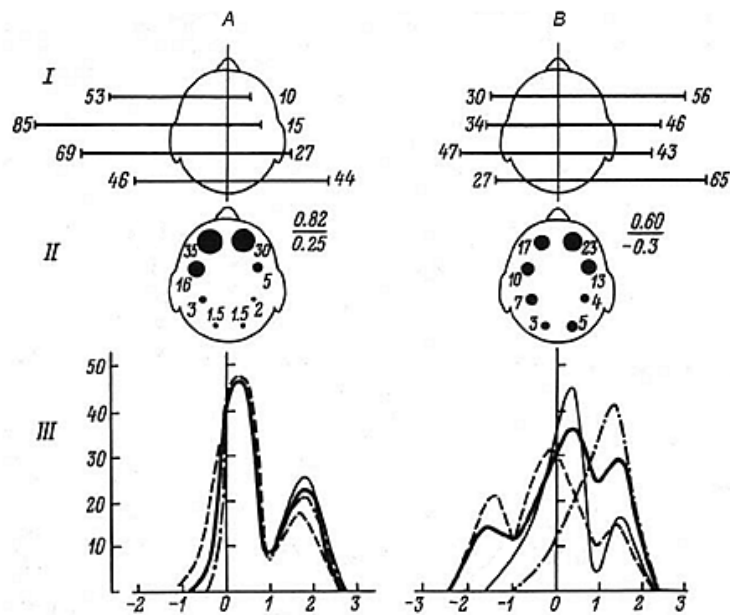

Figure 2. CAP types and mental work productivity at university exams (average data in 2 groups, 5 people in each). A—students with "excellent" results, generally high-achieving subjects; B—students with average or poor results, generally lower-achieving subjects. I—relative activation (by $K_{C/O}$) of left and right symmetrical cortical zones (%). II—regional activation indices (on hemispheric projections; conditional units); numbers on the right: numerator—anterio-posterior non-equilibrium ($K_{A/P}$), denominator—bilateral asymmetry index ($K_{L/R}$). III—variational distribution of $K_{C/O}$ values on logarithmic scale (on abscissa), number of variants ($n = 400$) for each value (on ordinate). One curve corresponds to one subject. Values within $K_{C/O} > 0$ reflect activation, values within $K_{C/O} < 0$ reflect marked inhibition, deactivation. For methods, cf Appendix 2.

Additionally, consideration of background EEG signals at the exam complements materials obtained by the EC/EO test, and allows to reveal symptoms of stress as well as mental fatigue in students. Most pronounced general cortical activation, determined by the coefficient of relative β- and α rhythm power ($K_{\beta/\alpha}$), was observed in stages II and IV of the exam, and was accompanied by most significant increases in pulse rate (by 1.5–2 times).

Below, we analyze the CAP types in two groups of students with most divergent results at the exam, respectively receiving "excellent" or "poor" (insufficient) grades. Both groups included five subjects, who were tested during the exam (by EC/EO test) no less than 60 times each. The high significance of obtained differences is reflected in the variational curves

obtained from large sample sizes ($n = 400$) of the EC/EO test in the two student groups (Figure 2).

In the "excellent"—graded group of students (Figure 2A), stable FMA was observed in left frontal areas by the general activation level as well as by the percentage of prevalent left-sided activity on the background of high anterio-posterior (fronto-occipital) activation gradients (AGs). At the same time, the almost complete superposition of $K_{C/O}$ variational curve values, revealing the presence of a distinct FMA in left frontal areas, testifies to a largely identical functional brain state in all five high-achieving subjects. Double-peaking variational curves reveal a distinct FMA in left frontal areas on the background of significantly reduced activation range in the subdominant brain regions, with a non-significant transition rate in the deactivated areas (by $K_{C/O} < 0$; cf. Appendix 2). This allows to speak of a correspondence between the identified CAP type and requirements posed by the given class of verbal-logical tasks.

Among students receiving average and poor grades (group B), no distinct and stable FMA was found on the background of predominantly right-hemispheric activity (Figure 2B). In this group, diverse types of individual variational curves are seen, as well as a wider range of functional states (FSs). There is significant variation in regions with increased ($K_{C/O} > 0$), as well as decreased activation, the latter reflecting an inhibited cortical FS ($K_{C/O} < 0$) (Appendix 2). Reduced mental working capacity is accompanied by predominant activity in right prefrontal areas, on the background of significantly diminished anterio-posterior AG.

Comparing exam stages IV and V—the oral response and post-exam rest (after the examiner has left)—leads to the suggestion that opponent-type functional states, as described by R. Solomon [1–3], characterize also cognitive performance during exams. This is reflected in the shifting activation indices for the left and right hemispheres, and accompanying changes in mood and feeling by FAM test (discussed below). During exam stage V, an interesting paradoxical reaction can be seen in the brain activity of highly anxious subjects: a state of defensive cortical inhibition characterizing the response period typically changes, after the examiner has left, to a relatively normal state with FMA in frontal cortical regions; at the same time, speech functions recover that had been suppressed in the student during the response period in the examiner's presence.

Below, a detailed comparison of functional brain states during key stages of the exam, I, IV and V, are shown for two most highly contrastive students (Figures 3 and 4; Table 1). The students belong to different grade groups (Figure 2): Student R. was the best among high-achievers, while student G. the poorest performer in the weaker group. Data on intra-individual and comparative time-series variation can be particularly informative given the non-Gaussian distribution of obtained within- and between group measures (Figure 2), as well as considering the marked variabilty of individual EEG indices across various stages of the exam (Figures 3 and 4).
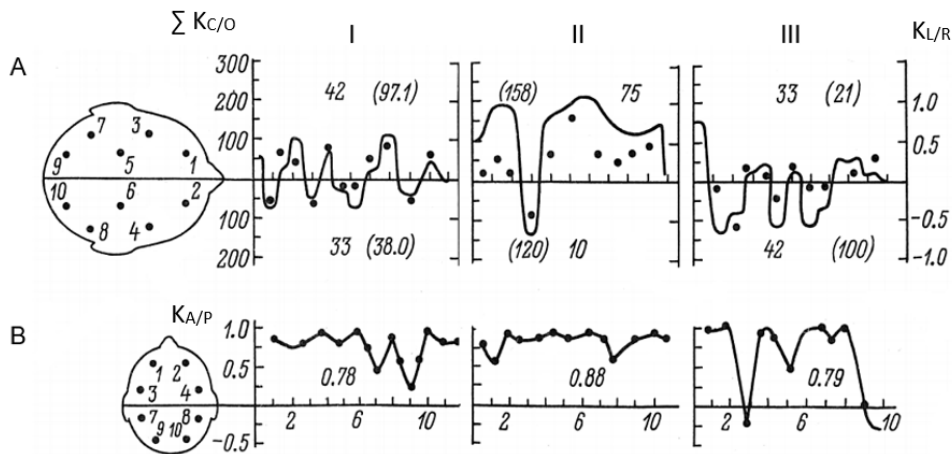
Figure 3. Examples of individual EEG dynamics during three examination stages in an excellently graded student (R.). A—diagram of the summed activation index of left and right cortical hemispheres ($\sum K_{C/O}$, left ordinate). Deviations above midline—functional predominance of left-hemispheric activity, below midline—right-hemispheric predominance; numbers above and below curves: in brackets—summed general cortical activation ($\sum K_{C/O}$), without brackets—relative activation predominance (%); isolated dots—values of inter-hemispheric asymmetry ($K_{L/R}$, right ordinate). B—magnitude of anterio-posterior non-equilibrium ($K_{A/P}$, ordinate); numbers below curves—averaged activation value; on abscissa—number of EC/EO trials (dots). I—before exam start; II—while answering the ticket; III—after exam termination (examiner has left). Differences in the scale for summed cortical activation in hemispheres (0–300) and their functional asymmetry (−1 to 1) are due to respective equations (measurement units are conditional) (Appendices 1 and 2).
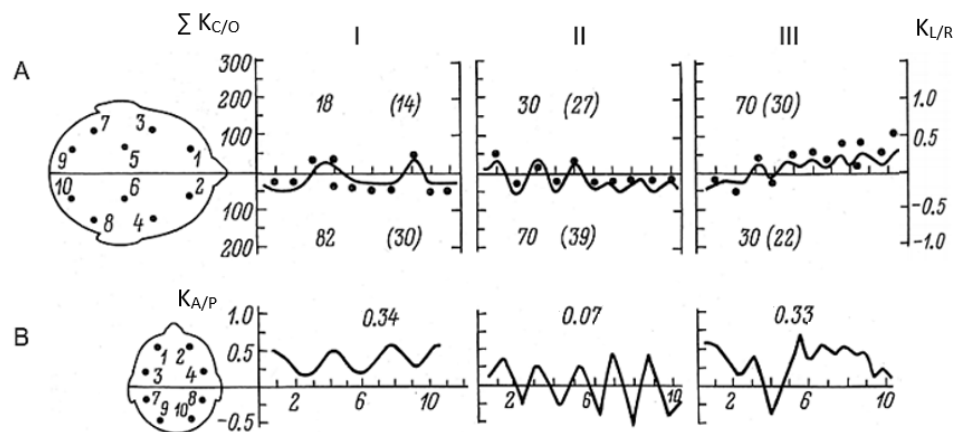

Figure 4. Examples of individual EEG dynamics during 3 examination stages in a poorly graded student (G.). Same designations as in Figure 3.

Table 1. Individual EEG, heart-rate and emotion indices of a highly-graded subject (R.) and a poorly graded subject (G.).

	Student R.			Student G.		
	I	IV	V	I	IV	V
Left hemisphere activation index	97	158	21	14	27	30
Left hemisphere dominance	42%	90%	33%	18%	30%	70%
Right hemisphere activation index	38	20	100	30	39	22
Right hemisphere dominance	33%	10%	42%	82%	70%	70%
$K_{L/R}$	0.4	0.7	−0.6	−0.3	−0.2	0.5
$K_{A/P}$	0.7	0.8	0.7	−0.3	−0.07	0.3
Heart-rate (bpm)	73	85	69	105	125	95
FAMai	6.0		4.5	2.2		5.3

Hemispheric activation indices are in conditional units (Appendix 2). I, IV, V—stage of experiment; $K_{L/R}$—bilateral asymmetry index; $K_{A/P}$—anterio-posterior asymmetry index; FAMai—FAM-test averaged scale index. Subject R. received an excellent evaluation, subject G.—poor evaluation.

Significant differences in the dynamics of cortical functional state can be seen in the representative highly-graded subject R. and poorly graded subject G. As seen on Figures 3–4, this difference is manifest already before exam onset, during the waiting stage (operative rest). This is reflected in the general level of cortical activation, which is significantly higher in student R. on the background of left-hemispheric dominance (shown as dots on Figures 3A, 4A), and the significantly higher (0.78) and more stable predominance of frontal cortical regions (Figures 3B, 4B). In student G., right-hemispheric dominance can be seen on the background of significantly reduced cortical activation and appearance on the EEG of slow hyper-synchronous delta-waves, reflecting cortical defensive inhibition already prior to exam onset. At the same time, anterio-posterior functional asymmetry is markedly diminished (0.34) due to deactivation of frontal brain regions.

These differences between students R. and G. increase during the response stage (II). In the high-achieving student R., left-hemispheric dominance is strongly amplified (with rising general activation), and the stability of frontal activity is increased. In student G., right-hemispheric dominance is retained on the background of reduced activation and instable dominance of frontal areas.

However, after exam completion, in both students rapid shifts occur in the opposite direction: in R., there is a transition to right-hemispheric dominance with a sharp drop in general cortical activation and reduced stability of frontal dominance, which can be interpreted as a reduction in neurocognitive work load. In student G., on the other hand, left-hemispheric

dominance is quickly increased after the examiner has left, together with increases in inter-hemispheric functional asymmetry and frontal activation, *i.e.* cortical activation is increased.

On the example of these two students, strongly opposed intra-individual functional brain states can be seen by EEG and pulse measures when comparing stages 4 (response) and 5 (examiner's departure) (cf. Table 1 and Figure 5).
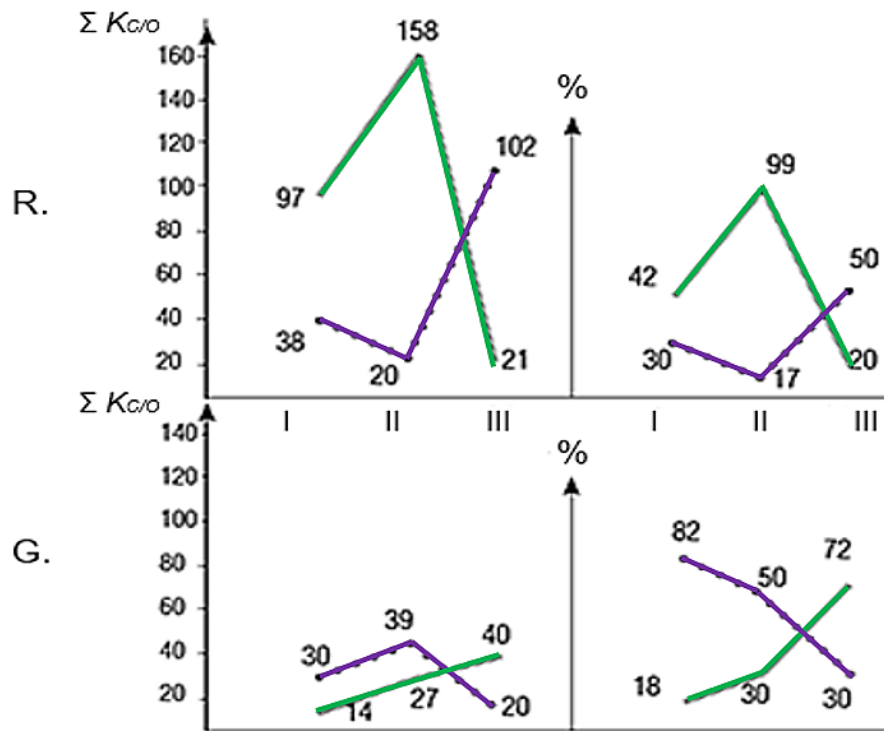

Figure 5. Prevalence of left- and right-hemispheric activation (by $K_{C/O}$) at three stages of the exam. Green—left hemisphere; purple—right hemisphere. Above—student R., excellent response. Below—student G., poor response. Abscissa: I—Initial state; II—response; III—after-effects. Left ordinate—activation sum by $K_{C/O}$ (curves in left columns); right ordinate—relative dominance of LH and RH, percentage (right columns).

Additionally, before and after the exam, we administered to all students the FAM test [41,42] on feeling, activity and mood changes (Table 1). The range of functional state (FS) shifts on this test lies on a scale from 1 to 6 points. Normal FS is considered to lie between 5.0–5.5 points; scores below 4 reflect poor FS and mood. In the high-performing group (Figure 2A), the average score prior to the exam was 5.5, and fell to 3.6 post-exam; in the unsuccessful group (Figure 2B) the average pre-exam score was 3.5, and rose to 4.9 after exam termination. In student R., the pre-exam score was 6.0 (highest in group A), but fell to 4.5 post-exam (by mood factor). In student G., the pre-exam score was 2.2 points; however, 20 minutes post-exam the score had risen to 5.3 (by mood factor) (Table 1).

Although these results are preliminary and need careful replication on larger samples, it should be noted that the corresponding changes in neural activity observed across task conditions in each group seem to confirm them. In particular, this concerns the widely reported associations of relative left frontal activation with positive emotions and approach motivation, versus the negative emotions and defensive motivation associated with right-hemispheric

frontal functions [28,44–46]. This asymmetry has also been directly observed in the context of examination stress regulation [10]. In this light, let us consider the two students' indices more closely.

Student R., with low anxiety, prevalence of verbal intellect, and analytical cognitive style (by Eysenck EPQ test), obtained an excellent grade. His initial functional state is characterized by left-hemispheric dominance, which increases during the exam response on the background of significant elevation of fronto-occipital AG and some increase in pulse rate. During this period, right-hemispheric activation decreases due to collateral inhibition from left-hemispheric dominants.

During the response, student R. shows positive emotions, apparently takes pleasure in answering the questions posed by the examiner. However, after responding, there is a clear drop in mood according to the FAM test (Table 1). At the same time, a significant reduction in left-hemispheric activation can be observed, together with increased activity and dominance of the right hemisphere, as well as diminished fronto-occipital AG, as shown in Table 1.

We can see from the above data how a clear transition takes place in student R., from a highly active physiological and cognitive state (and positive emotional experience) to an opposite functional state (accompanied by notably declined mood after the examiner has left). This is also reflected in the contrastive changes of EEG indices and pulse rate (Figure 5; Table 1).

Student G. shows high anxiety, has synthetic cognitive style, and prevalence of non-verbal intellect (by Eysenck's EPQ test). The subject knows the material, but has since school-years been afraid of exams. In the initial state, his cortical activity is reduced on the background of right-hemispheric dominance and markedly increased pulse rate (Figure 5; Table 1). Anterio-posterior AG and inter-hemispheric functional asymmetry are reduced. During the response, general cortical activation somewhat increases in the right hemisphere on the background of reduced activation and percentage of left-hemispheric activity, as well as deactivation of frontal regions (reflected in low fronto-occipital AG). However, as the examiner leaves, indices of functional brain state change contrastively—an increase is observed in left-hemispheric activation, together with increasing fronto-occipital AG on the background of collateral inhibition of the right hemisphere (Figure 5). In this case, a transition could be seen from negative emotional experience in the presence of the arousing stimuli (answering the ticket) to the appearance of a contrastive reaction—relief and satisfaction after the stressful situation has ended (as the examiner left).

A variety of methods were used to determine the emotional state of subjects. In addition to the oral response, the FAM test as well as certain behavioral characteristics and anamnesis were used. Student R., who received the excellent grade, had received during his two years of study at St.-Petersburg State University only the highest marks. Student G. did not manage to pass the exam and received a "poor"grade. During the response his speech was inhibited, and he did not seem to understand well the questions he was asked. Significant cortical deactivation was observed, and this coincided with markedly increased pulse rate (105 bpm) even before the exam, as well as during the response (125 bpm). This state can be defined as involving defensive inhibition ("functional pessimum") in the cerebral cortex on the background of simultaneous cardiac acceleration. It can be noted that this student, as well as others in the given group (Figure 2B), had frequent breakdowns during exams regardless of sufficiently good knowledge in the subjects. In all high-achieving students (Figure 2A), on the other hand, high mental productivity

and composure were observed on the background of stable left frontal FMA while answering the ticket.

Apparently, the reason for CAP "dissolution" in stressful conditions is related to excessive stimulation of the cortex by the ascending activating systems. This gives rise to a flow of tonic impulses that are amplified in conditions of novelty and stress, and remain insufficiently regulated by the cortex. According to Luria's [23] and many later studies [47,48], key functions in the top-down regulation of ascending activating impulses are fulfilled by frontal cortical structures—a view supported also by Kline et al.'s [28], as well as our own findings.

Furthermore, prior to the exam we tested both subjects by the Hand [43] and POI psychological tests. In student R., we found high directiveness (13 points) and high self-actualization (40 points); in student G.—high frustration (88 points), high anxiety (44 points), and low self-actualization (6 points).

From a methodological perspective, it may be revealing to compare the above results with the findings by Dayan et al. [42], who used the FAM test and cardiac activity measures to study examination stress among high-school students enrolled in general educational classes versus differential classes (with more intensive coursework). FAM test scores demonstrated different dynamics of FS change depending on the type of class the students were enrolled in, as seen in Table 2.

Table 2. Average FAM-test scores in students of general and differential education programs.

Measurement time	Average FAM scores in general program	Average FAM scores in differential program
Regular day	5.24 ± 0.22	5.09 ± 0.19
Pre-exam	**5.10 ± 0.25**	4.85 ± 0.17
Post-exam	**4.99 ± 0.25**	$4.95 \pm 0.29.$

FAM: Feeling, activity mood (test)

Thus, in the differential (intense coursework) class the scores were somewhat lower (4.85) than in the general class, possibly due to a sense of hightened responsibility for exam results. Higher examination stress was found in sympatotonics. However, in this study FAM scores were averaged across all students of a given class, without differentiating between highly and poorly performing subjects, as in our study. This may explain the less significant differences observed in the above summed FAM test results (Table 2). In other words, representative groups were not defined in either class by academic achievement motivation or actual progress, which may explain the differences from our findings.

Importantly, the above findings seem to indicate that processes with an opponent-type organization affect also higher cognitive functions dependent on strong motivational and emotional arousal. Of course, further similar studies including other groups of students and larger sample sizes are necessary to confirm and extend these findings. However, this should be done in representative groups (*e.g.*, highly motivated subjects), such as the reported groups of psychology students (all of whom were motivated to achieve high grades). Even then, regardless of possessing sufficient knowledge, some participants received low average or even poor grades since they were unable to concentrate, maintain composure, and cope with the

stresses presented by the examination setting. In high-performing students, stable left-hemispheric dominance and strong fronto-occipital activation gradients helped to cope with the stressful situation. In low-performing students, on the other hand, no distinct left-hemispheric and frontal FMAs were observed, and this resulted in lower grades and stress-resistance in the same objective examination setting.

In sum, the above results reveal marked differences in the CAPs of successful and unsuccessful students at the exam, as reflected in the significantly higher activation of left frontal regions in high-achievers and of right frontal areas in those who failed the exam or passed it poorly. However, it should be stressed that in both groups, the characteristic CAP structure was regularly replaced by a symmetrically opposite one, with the predominant FMA periodically shifting to the right hemisphere in high-achievers, and conversely, to the left hemisphere in low-achievers, depending on particular stages of the exam. These inverse changes were combined with changes in pulse rate and the affective state of subjects, as registered by the FAM questionnaire and judged subjectively by the examiners at the exam interview. Together with available data on the contribution of prefrontal regions to the lateralization of emotions [10,22,44–46], these results suggest a key role of frontal brain regions' dominance shifts in the task-specific regulation of motivational and emotional states, including their opponent dynamics [28].

Further, the obtained results show not only the relevant role of activational asymmetries in bilateral hemispheric regions, but also in anterior and posterior brain regions, the relative dominance of which must likewise be regulated in accordance with task settings. Increases in left frontal activity in high-achievers were coupled to decreased, highly structured and stereotypical activation of posterior brain regions. On the other hand, the activation of right frontal regions in low-achievers was associated with higher, more generalized and individually varied activity in posterior cortical areas. Thus, the CAPs revealed in high-achievers were found to be relatively uniform in distribution (Figure 2) compared to low-achievers, in whom higher divergence between individual variational curves was observed, reflecting a wider range of distinct cortical functional states (Figure 2). Similar results on the higher variability of EEG indices during the exam period in low-achieving students have been reported by Wiet et al. [14].

5. Discussion

The present study has shown that in exam settings, individually specific reorganizations of CAPs can be observed in students, accompanied by corresponding shifts in their motivational-emotional and cognitive processes. In the light of the opponent process model of homeostasis, we find the indications of dynamic "super-compensatory" effects in inter-hemispheric and anterio-posterior interactions to be particularly interesting, as observed in students under high work-load and exam stress conditions (Figures 3, 4). Thus, after periods involving high activation and relative dominance of either hemisphere or prefrontal regions, these functional activation indices are typically not simply downregulated to the baseline, but show a steep decline below it, accompanied by increased activation in the opposite hemisphere, or posterior regions (Figures 3, 4), in comparison to the initial functional state. This type of super-compensatory regulation seems not to be addressed in the classical frameworks of homeostasis, although as revealed by current and earlier related studies [1,3,28,29], it may represent a phenomenon of potentially wide adaptive significance in the self-regulation of

excitability in cerebral functional systems [22,28].[22] Theoretically, the opponent principle of regulation seems also consistent with current attempts to extend the classical frameworks of neural homeostasis by concepts such as anticipation and allostasis, to emphasize the inherent temporal variability and complexity of homeostatic processes in the brain [49–51].

Earlier, Craig et al. [29] investigated students' emotional dynamics during the high exam session, and found them to closely match Solomon's concept of opponent-type regulation. Our research has led to closely comparable findings. However, unlike in any prior studies, our study included integrated physiological and EEG measures, which were analyzed together with emotional and cognitive processes immediately in exam conditions, and while taking into account the various success rate of responders in high- and low-achiving groups. This is most important for distinguishing between the qualitatively different patterns of psychophysiological response expectable in subjects who not only achieve different grades, but who may experience the whole exam situation and challenge differently in terms of the motivational, stress-regulatory, and affective dynamics involved [9,52]. Indeed, in line with growing appreciation of the positive roles of stress in motivation and performance [53], Strack et al. [9] have recently shown how the stressful period immediately leading up to the exams can be experienced by some students as motivating rather than threatening or emotionally exhausting, indicating they interpret anxiety as facilitative to learning, and are less likely to appraise the exam stressor as a threat. While this ability is positively associated with academic performance, and prevents emotional exhaustion [9], it is also expectable that the opponent effects in such students would be manifestly different from those who experience the exam, or the days leading up to it, as primarily a negative and threatening stressor [9,52], with adverse health impacts [10,12].

Thus, although we have underscored the importance of differentiating between participants based on their performance to overcome such difficulties, there are further methodological and technical challenges to be addressed in this line of research. This includes, besides organizational difficulties, the relatively high diversity of motivational and emotional reactions involved in the exam situation, owing both to individual trait differences [30,54], as well as to individual expectations and experience in taking exams, the degree of preparation [55], and the subjective significance of the academic result [55,56]. For this reason, we enlisted only highly motivated and well prepared subjects in our study, and assigned them to different groups based on test scores before comparing the physiological data. Even then, besides group-averages, data on within-individual variability can be instrumental for understanding the neurocognitive structures and dynamics underlying successful and unsuccessful responses. In this way, the possible unique characteristics and strategies of responders can be characterized, together with their individual psychophysiological profile and state.

It should be noted here that most neurophysiological studies on opponent processes to date have looked at cases of pathological dysregulation, mainly addictive behavior and its underlying neurobiological circuitry, changes in which show obvious maladaptive dynamics—and probably involve pathological super-compensatory effects as described by the opponent-process model [57]. On the other hand, besides such obviously dysregulatory effects in neural substrates mediating motivational states [57], and other allostatic effects involved in pathology [49], the opponent type regulation seems to also reflect key principles underlying normal adaptation with a positive and adaptive temporal trend. For example, this has been revealed in

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[22]Interestinly, the problematic of super-compensation has a long history in Russian stress and sports physiology [87], as well as neurophysiology [25,88], although this has remained largely unknown in the West [5].

sports and physical exercise, the accompanying motivational and affective dynamics of which seem to reveal similar biphasic fluctuations, at least under more strenuous and intense exercise leading to increased resilience and stress tolerance (*e.g.*, *via* stress-induced analgesia by endogenous opioids) [58]. Recently, this biphasic dynamics has been associated also with increased frontal asymmetry measures on a possible opponent process basis [59,60], similarly as we demonstrate here for the exam setting. Together, this may allow to hypothesize a close integration between higher cortical, emotional, and bodily stress-regulatory responses, on the basis of shared or similar opponent effects in the neural circuits mediating them.

Before turning to more general theoretical and methodological implications of our findings, it is therefore appropriate to comment on their potential applied significance. Indeed, the facts obtained in the current study reflect not only theoretical concerns, but also practical interest regarding the functional diagnostics of students' functional state in educational settings, and in particular, prior to stressful tasks such as (oral) exams. This offers the prospect of detecting "risk groups" most prone to the possible adverse health effects of such educational tasks. Given the increasing rates of anxiety and stress among college students found in recent research [61–63], and their close relation to depression and other mental health problems [63], these have become particularly urgent requirements today, and are now challenging universities to continually evaluate the mental health of students, as well as to tailor programs of prevention and treatment sensitive to their individual needs and work specifics [61,63]. Based on the dominant principle and relevant findings, we can suggest several non-invasive measures to increase the resilience of cortical functions and work dominants in easily stressed, highly anxious, and chronically tired students.

(1) In students practicing sports, symptoms of cortical over-excitation or defensive inhibition were generally not observed during exams. This allows to speak of optimal relations between intellectual, emotional, and stress-regulatory components of the exam response in physically trained subjects [6], and is in accord with numerous findings on the neurocognitive benefits of exercise [64,65], even if its relations to opponent neural dynamics require further study [58,59]. In particular, defining universal dose-response relations between excercise vigor, motivational and affective opponent effects, and health benefits has remained a difficult and largely elusive task [58]. From the present perspective, this further underscores the need to develop methods sensitive to the individual variability and specificity of such integrated physiological responses. Below, we discuss this question in more detail with respect to EEG analysis.

(2) Development of self-control through neurofeedback [66–68]. Our results have shown increased neurofeedback effectiveness if, in each individual, a most "controllable" cortical zone is selected, in which the alpha-rhythm can be most easily amplified by neurofeedback signals through visual, or other feedback channels [69]. Neurofeedback sessions are found to increase the efficiency of mental work and optimize cognitive performance on the background increased left-hemispheric dominance and fronto-occipital activation gradients [6,46], in accordance with the above reported results.

(3) The stress impact of an exam can be reduced by changing how students are engaged— *e.g.*, by allowing a written reply, additional time for preparing responses, encouraging attitudes by the examiners, etc. In anxious and neurotic subjects this creates conditions for forming a sufficiently stable frontal left FMA and is accompanied by improved quality of the exam response [6,16]. Furthermore, we have found evidence for possible personal compatibility effects in student-examiner interactions based on the similarity of their resting-state

hemispheric dominance patterns [6,17]. The possible influence of such effects on a student's performance and grading should be taken into account, particularly in low-achieving students most prone to examination stress and anxiety.

Although traditionally, educational problems have been solved in the confines of humanities, the reported findings clearly indicate how a psychophysiological framework may support and enhance educational practices. This is particularly relevant for meeting special educational needs [16]. To best address these requirements, we propose that distinct types of integrative methods and concepts are needed to analyze not only inter-individual and quantitative, but also intra-individual and qualitative physiological measures of adaptation and human performance [70]. With regard to EEG analysis, this requires particular attention to the dynamic features of the EEG signal, such as its non-stationary stochastic properties [40]. While methods ignoring these complex properties have led to important discoveries, such as the functional specificity of individual EEG frequency bands, the initially rapid temporal resolution of the EEG signal is usually lost under such conditions [20,21], and makes its neurophysiological systemic interpretation more difficult. This limitation may particularly affect most dynamic experimental settings, such as those analyzed above, involving human psycho-social and socio-physiological functioning in exam conditions, or other conditions involving prolonged and conflicting motivational and stress responses.

In line with these requirements, we have presumed here that instead of individual frequency bands or correlational dependences between them, the neurophysiological units of cognitive processes should be sought in the rapidly shifting, discontinuous metastable states of the brain's biopotential field as a whole, characterized by anterio-posterior and inter-hemispheric activation gradients, as well as by global and regional changes in cortical states' inertial ("trace") properties (Appendices 1, 2). Such dynamic indices are highly variable both intra-and inter-individually, and this in close dependence on task conditions. Such methodological and methodical aspects may be fundamental if neuroscience research results are to be more directly applicable to educational settings and classroom scenarios, as currently called for [71]. Besides questions of methods and modeling, however, also ethical concerns should be further addressed in this line of research [72], including the possibilities of optimal educational and therapeutic interventions, preventive and rehabilitative measures at the individual level [16], as discussed above.

In our view, the framework of the dominant and the theory of opponent processes could provide valuable, mutually reinforcing concepts and models in this regard. These two frameworks are not only closely compatible, but both seem to possess the optimal levels of generality and complexity expected for integrative explanations and models in theoretical neuroscience [18]. Indeed, the necessity for such concepts—both sufficiently generalizable, yet well specifiable due to adequately chosen basic parameters—is becoming increasingly apparent in the field [18], together with some of the risks associated with prematurely formalizing its subject matter by methods drawn directly from other, non-biological disciplines (informatics, physics, etc.) [17,18,40,73]. These methodological considerations have played an important role in designing the current framework of EEG analysis on the basis of the dominant principle [6]. As such, it is hoped the presented materials encourage further research on the neural dynamics mediating opponent processes, and their integration into theoretical and applied human neuroscience.

Acknowledgments

Conflict of interest

The authors declare no conflicts of interest in this paper.

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Appendixes

Appendix 1

Work on the basis of the dominant model, as well as facts obtained by various analytical methods have revealed that the EEG correlate of cognitive states does not lay in individual frequency bands of the EEG signal, nor in the presence of correlational dependencies between them in any particular brain regions. Instead, it should be sought in specific metastable states of the cortical "bio-potential field" as a whole over subsequent time-segments [20,21].

Accordingly, we have developed methods for segmenting the EEG signals into intervals of structurally homogenous or uniform activation, separated by rapid transitions in the cortical field potential [17,40]. Similarly to current work on EEG "micro-states" and quasi-stationary structure [20,21], this approach is still relatively novel, as it avoids averaging EEG signals over extended time periods and broad frequency bands to achieve statistical reliability.

During structurally homogeneous EEG intervals, units of integral brain acitivity are identified as cortical activation patterns (CAPs), which are differentiated by the localization of foci of maximal activation (FMAs). Activation levels in distinct regions can be compared by spectral analysis of β-rhythm (excitation) and α-rhythm (rest) distribution, ($K_{\beta/\alpha}$), as illustrated on Figures 6 and 7.

The translocation and stability of FMAs in the cerebral cortex, corresponding to periods of structurally homogenous EEG intervals, are shown on multichannel EEG recordings (Figure 7), where the graphic analysis of their spectral characteristics is exemplified. Across diverse activities, we have found the phenomenon of α-rhythm "transfer" (translocation) (Figure 7) between bilateral symmetrical and anterio-posterior cortical zones to increase significantly under intense mental and physical work load, corresponding both to CAP type reconfigurations and functional displacements within a given CAP type. Thus, the intensity of brain activity and work dominants is expressed not only in the magnitude of activation reaction (coupled α-rhythm desynchronization and β- amplification, COD), but also in the speed of cortical EEG "mosaics" transformation. Fast FMA translocations and CAP reconfigurations are found in all experimental settings and psychological states, and prove to be significantly more expressed between bilateral symmetrical zones (switching dominant FMA every 1–2 s and faster) than in the anterio-posterior direction, although these parameters show marked individual specificity. Structural processing of EEG data shows the duration of structurally homogenous intervals not to exceed 0.25 seconds in a highly active cortex. On the other hand, on the background of relaxation and generalized α-rhythm amplification, the index of EEG stationarity can be seen to increase together with the decay interval of its autocorrelation function [40].

For selected EEG epochs, spectral analysis of β- and α-rhythm ($K_{\beta/\alpha}$) distribution needs to be carried out for all cortical zones from the same time-frame. Superposition of all obtained graphs (cf. Figure 6) enables to objectively analyze spectral characteristics of the EEG in various zones and to delineate FMAs.

The $K_{\beta/\alpha}$ coefficient can be expressed quantitatively in the following formula:

$$K_{\beta/\alpha} = \frac{\sum_{n=1}^{n\beta} A_\beta{}^{(i)} / T_B + 0.1}{\sum_{n=1}^{n\alpha} A_\alpha{}^{(i)} / T_B + 0.1} \cdot 100 \qquad (1)$$

where A_α and A_β depict oscillation amplitudes corresponding to α- and β-frequencies, respectively; and where T_B denotes time-periods of analysis.
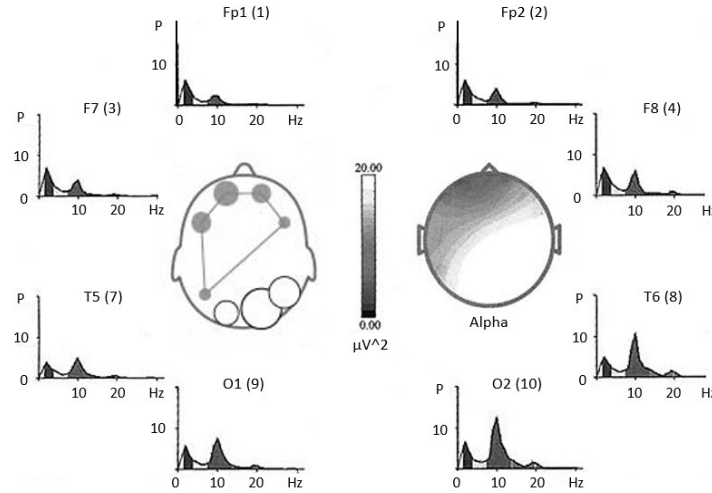
Electrode	Delta		Theta		Alpha		Beta1		Beta2	
	P μV^2	Hz	P μV^2	Hz	P μV^2	Hz	P μV^2	Hz	P μV^2	
Fp1 (1)	9.97	2.00	4.56	4.00	8.99	10.00	1.38	19.00	1.14	
Fp2 (2)	10.04	2.00	5.53	4.00	11.69	10.00	1.74	19.00	1.92	
F7 (3)	10.95	2.00	5.21	4.00	12.03	10.00	1.70	19.00	1.38	
F8 (4)	10.95	2.00	6.19	4.00	16.37	10.00	2.46	19.00	2.78	
T5 (7)	6.25	2.00	4.17	4.00	15.31	10.00	2.05	14.00	1.39	
T6 (8)	8.13	2.00	4.98	4.00	28.77	10.00	4.71	14.00	3.46	
O1 (9)	9.05	2.00	4.83	4.00	22.64	10.00	2.66	19.00	2.02	
O2 (10)	10.61	2.00	5.56	4.00	37.15	10.00	5.53	14.00	3.09	

Figure 6. Example of EEG spectral analysis (in 0.5 s periods). The table above displays oscillation power (P, in μV) across frequency bands and recording sites. The graphs depict oscillation frequency (Hz, abscissa axis), and power (P, ordinate axis). Projected circles on the cortical hemispheres (above, left) show temporarily dominant regions with heightened activation (black circes: β-rhythms), and areas falling under coupled inhibition (white circles: α-rhythm). The size of black and white circles reflects relative regional activation and inhibition magnitude, respectively. Electrode localization is designated both by the 10–20 system, as well as our own schema (numbers in brackets, Table above) (Appendix 3).
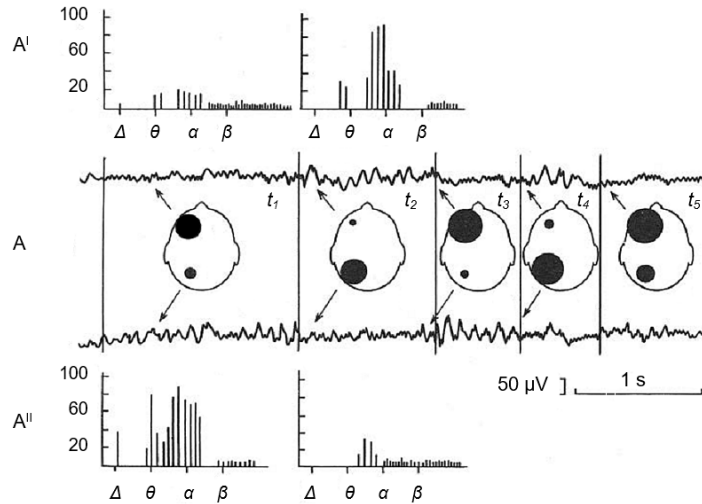
Figure 7. Graphic analysis of the spectral characteristics of structurally uniform EEG intervals (periods t_1–t_5). A—examples of EEG segments from frontal and temporo-occipital regions of the left hemisphere; A^I and A^{II}—spectral density graphs corresponding to the same recordings. Abscissa—oscillation frequency (Hz) of EEG waves, ordinate—their amplitude (μV). Black circle size on hemispheric projections reflects relative regional activation magnitude.

Appendix 2

The Eyes open/Eyes closed (EO/EC) test, described already by Hans Berger (1929), provides a simple and reliable means to assess quantitative differences in regional cortical activation [74]. It allows for functional testing of human brain states during highly engaged activity (such as oral exams), taking place on the background of highly desynchronized EEG and increased biological noise from various sources, such as interference from muscle potentials, corneoretinal potentials while blinking, *etc* [6], which drastically complicate background EEG analysis [75]. Experiments have shown that measures based on "activation reaction" in the EO/EC test convey identical information on the localization of maximal activation foci (FMA) as that given by spectral analysis of the $K_{\beta/\alpha}$ index [6].

Relaxational features of the β-rhythm (by EC) and the α-rhythm (by EO), *i.e.* the resetting speed of stationary regimes in oscillatory activity, are used to characterize excitation and inhibition inertia, and testify to the intra-cortical nature of these processes. This conclusion is based on comparing parameters of biorhythm frequency with the speed of synchronization and desynchronization reaction on the EC/EO test (Figure 8). In addition to latent reaction period (LRP) indices for EC/EO, we've employed the following activation coefficient:

$$K_{C/O} = \frac{LRP(EC)}{LRP(EO)}$$

(2)

where $K_{C/O} > 1$ is an active state within the range $1 < K_{C/O} < 300$; and where $K_{C/O} < 1$ is an inhibitory state within the range $1 > K_{C/O} > 0.001$.

In Figure 2, the values for $K_{C/O}$ are calculated by the normalized formula:

$$K_{C/O} = \frac{LRP(EC) - LRP(EO) + 0.1}{LRP(EC) + LRP(EO)} \tag{3}$$

where values within $K_{C/O} > 0$ reflect activation; and values within $K_{C/O} < 0$ reflect inhibition.
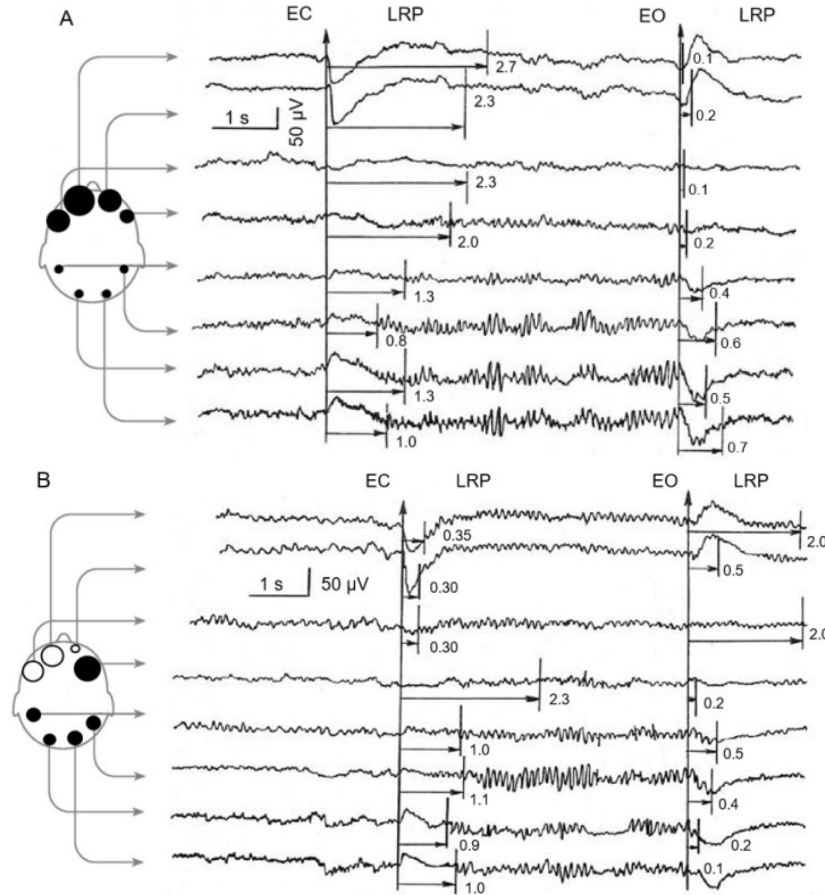

Figure 8. Two characteristic types of cortical activation patterns. A—executive function and logical effort (sequential analysis), dominance of frontal left brain regions; B—formation of images (simultaneous synthesis), dominance of posterior right gnostic regions. Levels of regional activation are calculated by LRP for EC/EO, the values of which are indicated by horizontal arrows and numbers (baseline 0 marks the appearance of corneoretinal potential by EC/EO). The size of black circles on hemispheric projections reflects relative regional activation magnitude; white circle size—relative inhibition magnitude.

Methods to determine ongoing cortical FMAs by using the EC/EO test, and methods to determine the extent and sign of functional asymmetry have independent significance. When comparing levels of cortical activation, functional asymmetry can be defined either by variational distrubution of $K_{C/O}$ curves, or by using alternative methods, such as calculating the number of cases with significantly higher left- or right-sided $K_{C/O}$ (at paired electrodes or inter-hemispherically). This has led to two groups of systemic EEG coefficients, characterizing cortical non-equilibria along anterio-posterior (fronto-occipital) (Eq 4) and inter-hemispheric (bilateral) (Eq 5) activation gradients.

$$K_{A/P} = \frac{anterior\Sigma K_{C/O} - posterior\Sigma K_{C/O}}{anterior\Sigma K_{C/O} + posterior\Sigma K_{C/O}}$$

(4)

where A/P denotes anterio-posterior asymmetry,

$$K_{L/R} = \frac{left\Sigma K_{C/O} - right\Sigma K_{C/O}}{left\Sigma K_{C/O} + right\Sigma K_{C/O}}$$

(5)

where L/R denotes bilateral asymmetry.

The coefficients K (A/P) and K (L/R) were also calculated by the parameter $K_{\beta/\alpha}$.

Appendix 3

In our EEG recordings we have generally not used the standard 10–20 system, but have preferred the R. U. Krönlein schema [76] to secure most accurate electrode placement on the speech zones of the left hemisphere. The method of symmetrical electrode placement developed by us on the basis of this schema [17,40] allows, by taking into consideration individual specifics of skull structure, to localize the speech zones of Broca and Wernicke with maximum accuracy, and thus to study their specific roles in regulating human activity.

The Krönlein schema is applied in the following manner (Figure 9, right). First, the lower horizontal (1) is determined, which passes through the lower margin of the eye socket and the upper margin of the external auditory canal. In parallel, an upper horizontal line (2) is drawn through the upper margin of the eye socket. Perpendicularly to these two horizontal lines are placed two vertical lines—the anterior vertical passes through the middle of the zygomatic arch, while the posterior vertical passes through the most posterior point at the base of the mastoid process. The projection of the central (Rolandic) fissure upon the skull is obtained by connecting two points: the first one corresponds to the intersection of the posterior vertical and the sagittal line, and corresponds to the apical end of the central fissure (Linea Rolandica). The second point is formed by the intersection of the anterior vertical and the upper horizontal (2), and corresponds to the lower end of the central fissure. The Linea Sylvii, which enables to localize the speech zones, is obtained by half-sectioning the angle between the Linea Rolandica and the upper horizontal, and extending the dividing midline till it intersects with the posterior vertical. The localization of Brodmann areas is taken into account in this schema (Figure 9, left).
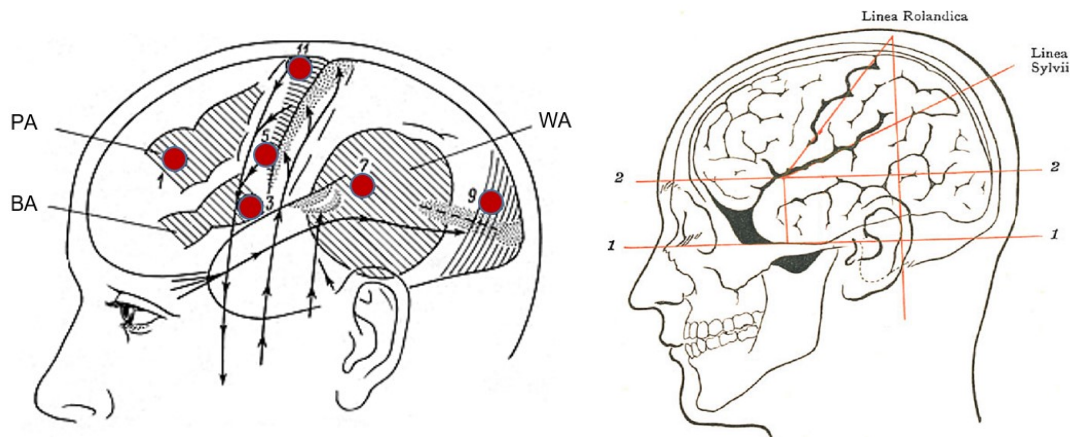
Figure 9. EEG recording sites and electrode montage. Left: Electrode placement on the left hemisphere. 1—prefrontal area (PA, Broadman area 46); 3—Broca's area (BA, Broadman area 44); 5—hand area; 7—Wernicke's area (WA, areas 39–40); 9—occipital area (visual fields 18–19). On the right hemisphere, electrodes 2, 4, 6, 8, and 10 are positioned symmetrically. Recording methods: unipolar, and with reference to the vertical top electrode, 11 (placed in front of the apical end of Rolandic fissure, on the interhemispheric fissure). Right: Krönlein's elecrode montage schema [6,40,76]. O—lower horizontal; P—upper horizontal; R—apical end of Rolandic fissure; B (1)—anterior vertical; B (2)—posterior vertical.