The musical centers of the brain: Vladimir E. Larionov (1857–1929) and the functional neuroanatomy of auditory perception

Lazaros C. Triarhou[1,*] and Tatyana Verina[2]

[1] Laboratory of Theoretical and Applied Neuroscience and Graduate Program in Neuroscience and Education, University of Macedonia, Thessalonica 54636, Greece

[2] Formerly, Department of Neurology and Developmental Medicine, Hugo W. Moser Research Institute at Kennedy Krieger Institute, and Department of Environmental Health Sciences, Johns Hopkins University Bloomberg School of Public Health, Baltimore, MD 21205, U.S.A.

*Corresponding author. University of Macedonia, 156 Egnatia Ave., Thessalonica 54636, Greece.
E-mail addresses: triarhou@uom.gr (L.C. Triarhou), tverina@yahoo.com (T. Verina).

Abstract

In 1899 a landmark paper entitled "On the musical centers of the brain" was published in *Pflügers Archiv*, based on work carried out in the Anatomo-Physiological Laboratory of the Neuropsychiatric Clinic of Vladimir M. Bekhterev (1857–1927) in St. Petersburg, Imperial Russia. The author of that paper was Vladimir E. Larionov (1857–1929), a military doctor and devoted brain scientist, who pursued the problem of the localization of function in the canine and human auditory cortex. His data detailed the existence of tonotopy in the temporal lobe and further demonstrated centrifugal auditory pathways emanating from the auditory cortex and directed to the opposite hemisphere and lower brain centers. Larionov's discoveries have been largely considered as findings of the Bekhterev school. Perhaps this is why there are limited resources on Larionov, especially keeping in mind his military medical career and the fact that after 1917 he just seems to have practiced otorhinolaryngology in Odessa. Larionov died two years after Bekhterev's mysterious death of 1927. The present study highlights the pioneering contributions of Larionov to auditory neuroscience, trusting that the life and work of Vladimir Efimovich will finally, and deservedly, emerge from the shadow of his celebrated master, Vladimir Mikhailovich.

Keywords:

Auditory cognitive neuroscience

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Vladimir M. Bekhterev (1857–1927)

Introduction

Advances in auditory neuroscience were made toward the end of the 19th century. Studies on the structure and function of the auditory and vestibular brain systems published since the 1880s by Hermann Munk (1839–1912) in Germany, Vladimir M. Bekhterev (1857–1927) in Russia, and others, have provided the biological foundations for the evolution of “otoneurology” as a neurological discipline (Arkhangelsky, 1984).

A Russian pioneer in the morphology and physiology of the cortical auditory system was Vladimir Efimovich Larionov (1857–1929). His work is largely forgotten, save the occasional mention by a small number of neuroscientists, historically versed. For example, the British-American physiologist Mary A. B. Brazier (1904–1995) of the University of California, Los Angeles (Brazier, 1960), the German-American electroencephalographer Ernst Niedermeyer (1920–2012) of Johns Hopkins University (Niedermeyer, 2005), and the New Zealander-American neuroanatomist Edward G. Jones (1939–2011) of the University of California, Davis (Jones, 2011), cited Larionov’s experiments in their writings, as has the psychologist Stanley Finger of Washington University in his narrative of explorations into brain function, in a chapter on audition and the central nervous system (Finger, 1994). Niedermeyer (2005), in particular, used the phrase, “Vladimir Efimovich Larionov conducted beautiful studies of the auditory cortex in the dog.”

Biographical sources on Larionov are scanty. A brief résumé concludes his doctoral dissertation (Larionov, 1898e). Beyond that, there is one Russian article referenced in Medline (Arkhangelsky, 1984), and a concise entry in the Encyclopedia of Modern Ukraine (Vasilyev, 2015).

A contemporary of Bekhterev (Fig. 1, upper), Larionov was born in Stavropol on September 19, 1857 (September 7 in the old-style Julian calendar). His father was a practicing physician and chief officer in Kazan. Russian Orthodox in creed, Larionov attended the First Imperial Gymnasium of Kazan, from which he graduated in 1876. In the same year, he was admitted to the Faculty of Medicine of Kazan Imperial University, from which he graduated in 1881.

In 1882 he began his military service as a physician at the Military-Medical Directorate of the Kazan District, being frequently seconded to the Kazan Military Hospital. During that period, he wrote several reports on organizational issues in military medicine (Arkhangelsky, 1984). Beginning in 1890, he specialized in otorhinolaryngology and became interested in the mechanisms of skull fractures; he published two papers (Larionov, 1891, 1897b), in which he attempted to interpret the type and location of such fractures on the basis of the principles of mechanics.

In 1893 Larionov obtained a Doctorate of Medical Science from Kazan University and was appointed senior physician at the 37th Dragoon Regiment (Larionov, 1898e; Arkhangelsky, 1984; Vasilyev, 2015). In 1895 he became senior registrar at the Military Hospital of Novogeorgiyevsk (today Svitlovodsk, Ukraine), whence he was seconded to the Military Medical Academy for the Advancement of Sciences. The following year, Larionov described a Menière-type syndrome when the Eustachian tubes are obstructed (Larionov, 1896). Until then, Menière syndrome was associated in the literature with purulent processes in the inner ear, and with hemorrhage in the semicircular canals and ear cerumen. At the conclusion of his article, Larionov was one of the first Russian physicians to describe diagnostic signs of the semicircular canals. He wrote:

> If suffering from the upper vertical canal, the dizziness is back to front or vice versa. If suffering from the outer horizontal anteroposterior canal, the dizziness will be about the axis of the body. When suffering from low posterior cross canal, the dizziness will be toward the affected side, that is, as if the head is leaning and the floor lowering from the affected side, while on the contralateral side, the floor will be as if rising. If the patient lies on the affected side, the head will feel like being lowered and the feet rising; and if the patient lies on the unaffected side, then it would appear as if the head is rising and the legs are lowered (Larionov, 1896; Arkhangelsky, 1984).

Larionov completed his doctoral dissertation (Fig. 2, left) in the Anatomy and Physiology Laboratory of the Clinic for Nervous and Mental Diseases directed by Bekhterev in St. Petersburg and successfully defended it at the Imperial Military-Medical Academy (Fig. 1, lower) on April 9, 1898 (Larionov, 1898e).

The opponent committee at the thesis defense comprised Bekhterev, the otorhinolaryngologist N. P. Simanovsky, and the psychiatrist A. F. Erlitsky. In his evaluation, Simanovsky emphasized the importance of Larionov's data, and noted that it is impossible to explain human brain activity based on experimental data from animals alone. Bekhterev, in his statement, highlighted the fundamental importance of Larionov's work, as it demonstrated that, in the auditory cortex, there is a specific arrangement for the perception of different pitches, as is the case for visual cortical areas (Arkhangelsky, 1984).

In his résumé, Larionov listed 13 published scientific works—including papers on the relation of rhinitis to the occurrence of otitis, and on the course and treatment of catarrh of the middle ear—which witnessed his experience in otorhinolaryngology. He also reported the design of an original eardrum perforator (Larionov, 1897a), as well as data on complications after mastoidectomy with the William Wilde retroauricular incision (Larionov, 1898f); Larionov claimed that mastoidectomy in purulent inflammation of the middle ear should be carried out as early as possible, and as close to the pinna underneath the suprameatal spine of Henle as possible, since nearby in this region is located the mastoid antrum of Valsalva, and there is a risk that the festering will spread.

Between 1902 and 1909, Larionov served as senior physician at the Kiev Military Hospital and as lecturer *(Privatdocent)* in the Department of Military Psychiatry and Neuropathology of the University of St. Vladimir in Kiev. Larionov became a member of the Russian Society of Physicians at the Imperial Novorossiysk University in 1911. For 1910–1912, he was appointed consultant and, for 1913–1917, chief assistant physician at the Odessa Military Hospital. After the Russian Revolution of 1917, and according to the physicians' directory of the U.S.S.R. for the year 1925, Larionov lived and practiced otorhinolaryngology in Odessa (Arkhangelsky, 1984); he was also affiliated, as *Privatdocent*, with the Odessa Institute of Medicine (Larionoff, 1926). He died in 1929 (Russian State Military-Historical Archive, f. 409, no. 2, doc. 28531) (Vasilyev, 2015).

Larionov published more than 40 scientific papers and monographs, mostly focusing on auditory neuroscience and neuropathology. He also authored a monograph on the acoustic secrets of old Italian violins (Larionov, 1910a). This latter publication (Fig. 2, right) appeared during the famous Odessa Expo of 1910. The industrial sections in the technological exhibition included art and production (painting, sculpture, musical instruments, design, furniture, interior decoration and so on). Larionov's text is written from the perspective of a violin master and offers violin construction details. The last paragraph mentions that the author exhibited violins made by him personally. Larionov (1910a) also mentions another maker of stringed bowed instruments who had presented his instruments at the Expo, Anatoly I. Lehman (1859–1913), who had studied and lived in Moscow and St. Petersburg. Lehman authored the "Book of the Violin" in 1892 and "Violin Acoustics" in 1903 (both published by Pyotr I. Jurgenson, the publisher of most of Tchaikovsky's works).

Perspectives in cortical tonotopy and the auditory centers

In 1881 Munk observed a loss of hearing in dogs, after destroying the cortical auditory fields in the perisylvian region bilaterally and by conducting hearing tests with organ pipes (Munk, 1881); he localized the principal focus at the ventral ends of the caudal ectosylvian and caudal suprasylvian gyri. Munk examined the ability of the animals to discriminate different pitches in a preliminary way; he conjectured that rostral lesions were associated with deficits in the discrimination of higher-pitch sounds and caudal lesions with deficits in the discrimination of lower-pitch sounds (Fig. 3.1). To Munk, the key region in the caudal ectosylvian gyrus was a center for the comprehension of the meaning of sounds, likening the effects of its removal to something resembling "psychic blindness" (Jones, 2011).

In 1895 the Swedish physician Johan Gustaf Edgren (1849–1929) suggested that the musical center in the human brain lies in the left temporal lobe, namely, in the anterior two-thirds of the superior temporal gyrus and in the anterior one-half of the middle temporal gyrus, rostrally to Wernicke's area (Edgren, 1895).

The first researcher who detailed the tonotopic acoustic map in the cellular organization of the cerebral cortex of the temporal lobe was Larionov (Fig. 3). He built upon and further refined the results of Munk by means of partial extirpations, and determined their cortical location for different high pitches (Wallaschek, 1900; Kalischer, 1910. His experiments did not accord with those of Munk regarding the localization of high- and low-pitch tones; he thus arrived at a reverse order of cortical localization in the temporal lobe for the various pitches (Henschen, 1919).

Larionov examined the components of the local acoustic reflexes to the action of various pitches by using precision tuning forks (Bechterew, 1909). He conducted extirpation experiments to determine the location of the auditory center in the canine temporal cortex and reported his first experiments in 1897 (Larionoff, 1897; Larionov, 1897c). He made small, circumscribed ablations of the temporal cortex in nine dogs and checked their hearing before and after the operation. The perception of any sound was indicated by a turning of the head or the eyes, motion of the ears, and so forth.

Shortly after a unilateral extirpation (2–3 days), the dogs became deaf and did not respond to chamber sounds. Within the following week to a month, the dogs began to respond to sounds received by the contralateral ear and, somewhat later, partially to those received by the ipsilateral ear as well. Based on that finding, Larionov deduced that each ear is connected to the cortical auditory centers of both cerebral hemispheres, contrarily to Munk, who had held the view that the auditory pathway from the ear to the temporal cortex of the dog is exclusively crossed. Larionov concluded that the center for high notes lies in the angular gyrus, for middle octaves in the ectosylvian gyrus, and for the low octaves in the suprasylvian gyrus. [The gyrus angularis or gyrus sylviacus of the cerebral cortex in the dog brain is homologous to the posterior ventral part of the insula in the primate brain (Figs. 3.2 and 3.7); the gyrus angularis of the dog is not the same as the gyrus angularis in the parietal lobe of the human and ape brain (Bechterew, 1911).] In essence, Larionov clearly formulated in his conclusions that pitch perception in the auditory cortex repeats the tonotopy observed in the cochlea (Larionov, 1897c; Flatau, 1898). Today we know that tonotopic organizations exist in the auditory cortex, the medial geniculate body, the inferior colliculus, the superior olivary nucleus, and the cochlear nucleus of the acoustic nerve (Netter, 1977).

In 1898 Larionov published another paper on hearing and the auditory pathways (Larionov, 1898b), which was also reprinted as a separatum (Larionov, 1898c). He used the Marchi method to trace nerve fibers undergoing anterograde degeneration. He noticed, after lesions around the Sylvian fissure, degenerated centrifugal axons originating in the primary auditory cortex, coursing along the primary auditory pathway, and directed to the outer and inner parts of the lentiform nucleus, contralateral external and internal capsule, corpus callosum, subcallosal fascicle of Muratoff, and caudate nucleus (Larionov, 1898b; Niessl von Mayendorf, 1914). He further traced degenerated axons in the outer portion of the thalamus (stratum zonale), medial geniculate body, posterior commissure, nucleus of Bekhterev (superior vestibular nucleus of the acoustic nerve), anterior decussation, posterior longitudinal fasciculus, and medial aspect of the reticular formation, as well as the cerebellar peduncles, and the temporopontine and occipitopontine fiber tracts. Thus Larionov discovered the efferent pathway from the primary auditory cortex, through the corpus callosum, to the contralateral temporal cortex, and also corticofugal fibers from the auditory cortex to the root of the acoustic nerve. Studies conducted decades later confirmed and expanded upon these discoveries (Tunturi, 1952, 1960; Hind, 1953; Kachuro, 1963; Evans, 1968; Goldstein, Abeles, Daly, & McIntosh, 1970; Tunturi & Barrett, 1977; Yost & Nielsen, 1977; Arkhalngelsky, 1984).

The results of Larionov's experiments on the auditory system of the dog culminated in his doctoral thesis (Larionov, 1898e), a formidable work in auditory neuroscience. The first part (chapters

I–VII, pages 3–88) is a comprehensive historical introduction and a still useful review of central and peripheral mechanisms of auditory and vestibular functions, from antiquity through the end of the 19th century. The experimental part (chapter VIII, pages 89–289) presents the data from 20 experiments on tonotopy in the canine auditory cortex. Chapter IX (pages 290–294) is a focused discussion of the results in a neuroanatomical context. Chapter X (pages 295–345) critically reviews the literature on amusia, and chapter XI (pages 346–368) that on verbal deafness. The thesis ends with the conclusions (Table 1), a biosketch with a list of publications (pages 371–372), and 13 plates with 115 figures.

The following few paragraphs summarize the main points of the thesis. One to two days after the removal of even small pieces of temporal cortex from the suprasylvian, ectosylvian or perisylvian gyrus, the hearing of tones or sounds from the contralateral ear is markedly diminished or completely lost, whereas the effect on the ear ipsilateral to the lesion is less pronounced. This indicates a partial decussation of the acoustic nerves, whereby each ear is connected by a larger number of fibers to the crossed tonal cortical centers and by a smaller number of fibers to the uncrossed cortical centers. Such a pattern was explained by the degeneration of association, commissural and projection auditory pathways in both cerebral hemispheres and on both sides of the midbrain, as documented in histological preparations processed with the Marchi method. Hearing is restored in both ears with the exception of certain pitches for which hearing remains somewhat impaired in the ipsilateral ear and greatly weakened or completely absent in the opposite ear.

The areas of the temporal cortex that perceived pitches of different frequency were unequal. When the caudal parts of the angular, the ectosylvian or the suprasylvian gyrus were destroyed, there was a dissipation, respectively, of high, middle or low octaves (Figs. 3.3 and 3.6). If all three gyri were removed as a transverse strip, then the pitches of all six octaves fell out, with the exception of intermediate non-dropped pitches, by which it was possible to hypothesize the course of the tone scale in the temporal gyri (Figs. 3.4 and 3.5).

The cell groups for ascending pitch scales in the auditory cortex are arranged as follows: the tonal centers for the lower octaves toward the centers for the higher octaves begin at the caudal segment of the suprasylvian gyrus from top to bottom; they skirt round the bottom of the caudal end of the suprasylvian sulcus into the ectosylvian gyrus, where they are arranged from bottom to top; upon reaching the middle of this gyrus, they turn down, through, or rather underneath, the ectosylvian sulcus, into the caudal one-half of the angular gyrus, and also course from top to bottom (Figs. 3.3 and 3.6).

The results showed that there is a center for the perception of a pitch scale that corresponds to the pitch scale of the cochlea. Extirpation of the caudal one-fourth of the second (suprasylvian) temporal gyrus led to a loss of response to the low pitches between A_1 and E; of the caudal one-third of the third (ectosylvian) temporal gyrus, to the middle pitches from G_1 to B_1; and of the caudal one-half of the fourth (perisylvian or angular) temporal gyrus, to the high pitches, from C_2 to C_3 and higher (Figs. 3.3 and 3.6).

Important questions concerning the fine localization of pitch centers and the sequence of the central tone-scale, as concluded from these experiments, complemented and developed the original idea of Munk based on the perception of different pitches by different auditory centers in the dog, by demonstrating the exact location of the pitch centers in the sequence of a six-octave diatonic scale in the three adjacent temporal cortical gyri.

As far as the perception of *sounds* is concerned, these fell off in parallel with the perception of *pitches* in multiple experiments. Larionov assumed the existence of a rudimentary center corresponding to Wernicke's area in the dog brain, because, even after a fallout of responses to almost all pitches and sounds, the perception of *speech sounds* did not dissipate. Such an area is likely located at the top of the middle ectosylvian gyrus.

In control experiments, with lesions of the frontal or parietal lobe, hearing was not affected. Such a finding was in agreement with the experiments of Tonnini (1898).

Lastly, the faradic stimulation of the three cortical gyri mentioned above and responsible for hearing, elicited movements of the animals' ear, eye and head muscles bilaterally. Upon cortical stimulation with electrical current, the ears, eyes and head were tilted toward the opposite direction, as if the animals were listening with the opposite ear (similar to the "subjective auditory sensations" of Ferrier). This is the "auditory reflex," often mentioned in experimental studies on the inferior colliculus, noted in Larionov's experiment 16, and also by Bekhterev in his own experiments; rotation of the ears, eyes and head also occurred after current stimulation of the superior colliculus.

Regarding the "psychic deafness" *(Seelentaubheit)* of Munk, Larionov's four final experiments did not support that view. With the removal of the cortical auditory centers, the dogs were startled, initially becoming very fearful, and "reminiscent of patients with mental retardation"; they recovered promptly, however, and were able to follow verbal orders without the use of gestures (such as "serve," "up," "give a paw"). It is conceivable that Munk had destroyed the suprasylvian gyri substantially higher, separating the auditory center from the posterior associative center of Flechsig and consequently mimicking a transcortical verbal deafness; in other words, his cortical lesions spread back and they might have also affected the posterior associative center, thereby causing the psychic deafness.

Within a few months, the dogs that had been operated on became almost completely deaf owing to the diffusion of the brain softening into regions adjacent to the auditory centers, and as a result of the degeneration of auditory fibers, both association and commissural, connecting temporal regions of the two hemispheres, and also projection fibers in both hemispheres and on both sides of the brainstem. This was shown by histopathological studies of the animals' brains, as well as by the work of Muratoff (1893), who pinpointed the degeneration of callosal fibers extending from the lesion area to the corresponding area in the opposite hemisphere.

A few months after his thesis defense, Larionov presented his results in a lecture before the Scientific Meeting of the Physicians of the St. Petersburg Clinic for Nervous and Mental Diseases on

September 24, 1898 (Larionov, 1898d; Larionow, 1899b).

To confirm his findings on tonotopy, at the instigation of Bekhterev, Larionov used the fluctuations of cortical currents for the localization of the auditory sphere of the dog (Berger, 1929). Larionov's inventiveness led him to record responses to tuning forks of different pitches by placing a galvanometer on the cortical surface to determine the localization of the auditory areas (Jones, 2011). Upon learning of the success of Richard Caton (1842–1926) with visual stimuli, Larionov took up the problem of localization and conducted experiments by using a procedure similar to what is referred to today as auditory evoked potentials (Larionov, 1899a; Larionow, 1899b). His findings confirmed Caton's observations on electrical brain responses after sensory stimulation, something that Hans Berger (1873–1941) had not been able to do (Brazier, 1960). Apparently, Larionov had a more sensitive instrument (a Wiedemann-d'Arsonval galvanometer) than his predecessors, and was thus able to map out the topographic centers on the temporal cortex of responses to different pitches (Brazier, 2012).

Larionov suggested that the homologous musical center in the human brain should be located in the posterior insula and the anterior parts of the superior and middle temporal gyri. He promptly confirmed his beautiful physiological work—somewhat daring in its final conclusions, as it was based on experiments in dogs, in which it is not easy to exclude subjective errors—both with anatomical studies and through clinical observations, which proved the specificity and the autonomy of cerebral musical ability (Bogdanof-Berezovsky, 1900).

He wrote that the "word center" of the dog is in a primordial state. It lies in the middle one-third of the left third (ectosylvian) temporal gyrus. In the article "On the musical and tonal centers of the brain," Larionov claimed that the musical center perception in humans is located close to Wernicke's area, namely, in the anterior two-thirds of the superior temporal gyrus, and the posterior part of the insula (Larionov, 1899c; Larionow, 1899a). Larionov agreed with Flechsig that the auditory tracts are bilateral in the cerebral hemispheres (Brace, 1899; Wallaschek, 1900).

The anatomist August Knoblauch (1863–1919) had implicated five modules involved in music processing: the three primary centers were the "auditory center for tones," the "motor center for tones," and the "center for ideas"; the other two were the "visual center for notes" and the "motor center for music notation-writing." Most of those centers were proposed to be modality-specific and to solely process music information. The only modality-nonspecific center was that for ideas, as it processed multiple types of information (Johnson & Graziano, 2003).

Larionov, after further study of the human brain, located the center for "note-reading" with the common reading center, the center for "note-writing" with the word-writing center, the "song center" slightly posterior to Broca's motor speech area at the foot of the left inferior frontal gyrus, and the center for "musical idea conception" in the left frontal lobe near the anterior associative center of Flechsig. The left "tone center" and Wernicke's area are distinct from each other and have separate fiber tracts (Brace, 1899; Wallaschek, 1900).

Subsequent studies on the distortion of ear for music affirmed that amusia results from lesions in the right temporal region (Feuchtwanger, 1930; Luria, 1966). After reviewing pathophysiological studies, Economo (1927, posthumous English edition 2009) concluded in the 1920s that the center for the understanding of word phonetics (“verbal audition”) was localized in the cortex of the posterior superior temporal area TA_1 of the left side (Economo & Koskinas, 1925, posthumous English edition 2008); the center for the understanding of word meaning (“verbal cognition”) in the caudal transition area from TA_1 to PF; and the center for the understanding of music (“musical intelligence”) in the anterior superior temporal area TA_2—further subdivided into fields T$A_{2\alpha}$ and T$A_{2\beta}$ by Economo and Horn (1930)—and perhaps even in the left temporal pole.

The Swedish neurologist Salomon Henschen (1847–1930), after showing that the macula of the human retina projects to just one part of the visual cortex, postulated based on his clinical cases, that there was a comparable orderly arrangement for sound frequencies at the cortical level (Henschen, 1918).

The resultant map of Larionov was a remarkable facsimile of the cochlea (Larionow, 1899a), with higher pitches represented dorsocaudally (Figs. 3.6 and 4). His lesions potentially penetrated different parts of the acoustic radiation and might have interfered with the tonotopically organized thalamocortical projection to the primary auditory areas, which we now know to be located more dorsally in the ectosylvian area (Jones, 2011).

Detailed studies on the electrophysiology of the auditory cortex appeared in the 1940s (Finger, 1994). By stimulating different parts of the cochlea and recording from different parts of the temporal lobe, Woolsey and Waltz (1942) observed a specificity in the connections from the cochlea to the auditory cortex of the cat. The tonotopically organized region, found at the cortical level with the base of the cochlea represented rostrally, was supplemented by a second tonal map, located ventrally to the first, with the sound spectrum in reverse order (Woolsey & Fairman, 1946). Those two regions were defined as temporal areas AI and AII (Finger, 1994). In the cat, low pitches are transmitted to the frontal end, and high pitches to the occipital end of the acoustic area. In humans and primates, the twist by which the temporal lobe develops ontophylogenetically has brought about a reversal in the location of high and low pitches (Ades & Felder, 1945; Netter, 1977). Whereas the temporal cortex is necessary for most aspects of sound localization (Whitfield, Cranford, Ravizza, & Diamong, 1972; Heffner, 1978), the auditory cortex is not essential for frequency discrimination, as cats are able to perform this provided that the auditory midbrain and the inferior colliculus are intact (Goldberg & Neff, 1961; Jones, 2011).

In the cochlea of the human ear, low pitches are picked up near the helicotrema (tip), and high pitches near the oval window. From the medial geniculate body, the acoustic radiation emerges to end on Heschl’s gyrus on the supratemporal plane. There is a point-to-point correspondence between the cochlea and the auditory cortical area on Heschl’s gyrus on the supratemporal plane. In humans and the other primates, high pitches are transmitted to the frontal end of the acoustic area, and low pitches to the occipital end of the acoustic area (Netter, 1977). Excitations of the hair cells are transmitted to the cochlear division of the acoustic nerve, its fibers entering the brainstem at the lateral side of the pons, lateral to the restiform body and immediately split up to enter the dorsal and ventral cochlear nuclei (Lorente de Nó, 1933a, 1933b). The further cell stations of the auditory pathway to the cortex are the superior olivary nucleus, connected via the lateral lemniscus to the inferior colliculus, and the medial geniculate body. Many, but not all, fibers decussate. Of the decussations, the most ventral at the level of the superior olive is the strongest, known as the trapezoid body.

In modern studies using functional magnetic resonance imaging (fMRI) to investigate the tonotopic organization of the human auditory cortex, activations for high-frequency pitches were located more posteriorly and medially than those for low-frequency pitches (Wessinger, Buonocore, Kussmaul, & Mangun, 1997). Low- to high-frequency spatial gradients were discernable along Heschl's gyrus and sulcus in an anterolateral to posteromedial direction; in the primary auditory cortex, activation was systematically strongest in response to contralateral stimulation (Langers, Backes, & van Dijk, 2007). Further studies with fMRI reinforce the idea that tonotopy is the most prominent organizational principle in the auditory pathway, with some aspects of the layout of tonotopic maps in the human brain still being open to discussion. Neuroimaging data indicate the existence of two tonotopic maps that run diagonally across the anterior and posterior banks of Heschl's gyrus at a pronounced angle (van Dijk & Langers, 2013). Similarly, it has become apparent that the human auditory cortex comprises multiple subfields; tonotopy extends along two axes, one oriented medial to lateral along Heschl's gyrus, and the other anterior to posterior (Leaver & Rauschecker, 2016). Regions with preferential responses to the human voice and speech occupy in particular low-frequency portions in the cortical tonotopic map, while such speech/voice selective regions exhibit a response bias toward the low frequencies that characterize human voice and speech, even when responding to simple tones (Moerel, De Martino, & Formisano, 2012).

Cortical tonotopy and conditioned reflexes

A decade after the publication of his thesis, Larionov again became interested in temporal cortex tonotopy. Two dissertations had been completed in 1908 in the laboratory of Ivan P. Pavlov, by I. S. Makovsky ("Sound reflexes after removal of the cerebral cortex in dogs") and by M. E. Elyasson ("Research on the hearing ability in dogs under normal conditions and after partial bilateral removal of the auditory center"). Both works helped to cast doubt among Russian neurologists on the reliability of Larionov's earlier data on temporal cortex tonotopy, despite the fact that neither of those theses directly refuted his experiments (Arkhangelsky, 1984). To corroborate his own data, Larionov conducted experiments by recording conditioned reflexes, using tuning forks and odors as the unconditioned stimuli, and published the results in two papers.

In the first paper, Larionov (1910b) scrutinized the methods of Makovsky and Elyasson and noted the controversial and weak aspects of their experiments. Larionov stressed the distinction between sound stimuli (harmonium, piano, electric bell, whistle, noise, organ pipes) used by Makovsky and Elyasson, on one hand, and his own precision stimuli of tuning forks, on the other. He criticized the stimuli adopted by Makovsky and Elyasson as lacking a gradually quenching attribute. Larionov further, and accurately, pointed out that Makovsky and Elyasson had not removed the auditory cortex completely, but had spared part of it and, accordingly, part of the tone scale perceiving area, which led to reflexes to low pitches.

In the second paper (Larionov, 1910c), which he read on April 23, 1909 before the St. Petersburg Society of Russian Physicians, Larionov presented data on the possibility of getting conditioned reflexes to tuning fork stimuli combined with odors. He argued that such a combined approach would be more appropriate for investigating tonotopy in the temporal lobe than studying conditioned reflexes by measuring salivation alone. In the same work, he provided evidence that olfactory conditioned reflexes could be still observed, after removing the olfactory bulb surgically, and, based on those observations, suggested that olfactory stimuli are transmitted along the trigeminal nerve. He gave an original schematic drawing of the olfactory areas and pathways; this was one of the early depictions which helped to further develop the scheme of the olfactory circuit.

That presentation took place at the height of the "battle of titans," the bitter public duel that escalated between a temperamental Pavlov and a forceful Bekhterev between 1906 and 1909 (Todes, 2014). In a faculty meeting at the Imperial Military-Medical Academy a month earlier, Pavlov, disdaining the laboratory's experimental procedures and results, had announced that he would no longer participate on the doctoral committee of Bekhterev's students. Bekhterev had earlier resigned from the doctoral committee of one of Pavlov's students, due to his distrust of the "striking overestimation" of research on the brain which relied heavily on Pavlovian conditioned reflexes.

The clash of Bekhterev and Pavlov was deeper and older, conceivably rooted in their concurrent student years. It is common knowledge that later, as professors at the Imperial Military-Medical Academy, they avoided saying "hello" to each other when they met in the corridor. After Pavlov described his conditioned reflexes, colleagues bitterly joked that, in his relation with Bekhterev, Pavlov himself was a perfect example of conditioned reflexes.

Both titans participated in the session of the Society of Russian Physicians in April 1909 for yet another heated confrontation. Pavlov invoked his winning of the Nobel Prize. Bekhterev decried Pavlov's argument from authority and dropped the argument that his rival had won the Prize for studies on digestion, not on the brain (Todes, 2014).

It was Larionov (1910c) who took center stage and defended Bekhterev, by reporting problems in Pavlov's method, such as the appearance and disappearance of salivary conditioned reflexes for unknown reasons, and their possible subcortical, rather than cortical, origin; with such complex dynamics, these reflexes, instead of offering an objective reflection of cortical function, inescapably confounded researchers with vagueness. Larionov's legitimate arguments forced Pavlov and his colleagues to grapple with some of them. Nonetheless, Pavlov dismissed Larionov's paper, and commented that most of the arguments would appear novel only to "the presenter, who has been working in the province" (meaning Kiev). Pavlov's colleague I. V. Zavadsky reported that, contrary to the findings in Bekhterev's laboratory, ablation of the piriform gyrus led to specific changes in conditioned reflexes to scent, but not to their total or permanent disappearance. These were also meaningful data, but, instead of debating them, Bekhterev lectured Zavadsky on the dangers of operating on the brain with a submarginal knowledge of neuroanatomy (Todes, 2014). For the sake of history, we mention that Bekhterev was nominated ten times for the Nobel Prize in physiology or medicine between 1912 and 1925 (www.nobelprize.org/nomination/archive). Pavlov, as a former laureate, refused to endorse Bekhterev's nomination.

Distinct pathways for language and music in the brain

The problem of the existence of a musical center in the brain was first brought up by Charcot in his Friday lectures of 1883–1884 at La Salpêtrière, after dissociating aphasia from music disorders, (Arkhangelsky, 1984). Charcot actually proposed four centers for music in the brain, different from the centers for language: such centers underpinned music auditory images, music visual images, music articulation images, and music writing images (Johnson, Lorch, Nicolas, & Graziano, 2013).

In 1888 Knoblauch proposed a diagrammatic "cognitive" model of music based on the language diagram of Ludwig Lichtheim (1845–1928), and further introduced the term "amusia" and proposed nine forms of music production and perception disorders (Knoblauch, 1888; Johnson & Graziano, 2003). Subsequently, the Austrian psychologist Richard Wallaschek (1860–1917) described two levels of conceptual music processing, "tone representation" and "music representation," and distinguished six forms of amusia: motor amusia, sensory amusia, paramusia, musical agraphia, musical alexia, and musical amimia (Allen Starr, 1894; Graziano & Johnson, 2015). Knoblauch suggested that the "auditory center for tones" is near the superior temporo-sphenoidal gyrus (superior temporal lobe), and the "motor center for tones" is near the inferior frontal gyrus or Broca's area in the left cerebral hemisphere (Johnson & Graziano, 2003).

Pursuing his aim to establish the location of a musical center in the brain, Larionov studied tonotopy in patients with aphasia (Larionov, 1898a). In the St. Petersburg Clinic for Nervous and Mental Diseases, he observed two patients suffering from transcortical sensory and motor aphasia with preservation of musical abilities in the one patient. The study, using tuning forks, showed that the patient could perceive all tones of the octave and precisely execute the entire voice range (Larionoff, 1898; Larionov, 1899d; Larionow, 1899c).

In the scientific session of the Physicians of the St. Petersburg Clinic for Nervous and Mental Diseases on January 8, 1898, Larionov demonstrated the cases of the two patients, with a clinical picture similar to the classic cases of Otto Heubner (1843–1926) nine years earlier. The two cases were carefully analyzed, but without an autopsy. There was a lack of comprehension of most words, a virtually complete absence of volitional speech, with paraphasia and a fully developed alexia and agraphia; all this was accompanied by a complete preservation of the ability to repeat words. One of the patients could chant the Russian anthem and then repeat the lyrics. Larionov classified the cases in the category of transcortical aphasia, according to the diagrams of Lichtheim and Wernicke, and interpreted them based on the schemes of Lichtheim and Knoblauch, while also referring to the associative centers of Flechsig (Larionow, 1899c; Raïchline, 1900).

The lower reflex arc of language, with the areas of Wernicke and Broca and their conductors, was not altered. These areas are separate from the center of objective comprehension (posterior associative center of Flechsig), since the patients could neither understand the words they were told (which they repeated) nor speak on their own initiative. Such patients, although in the long run can remember a few words and point to and learn some objects, are usually condemned to silence. The observations proved that fascicles (a) from Wernicke's area, which go to the posterior associative center and from the latter to Broca's area, and (b) of the center of visual images of letters and words (angular gyrus), which go to the motor center of writing (middle frontal gyrus) and to Broca's area and subserve writing and reading, course close to each other. That is why they are affected simultaneously. The arcuate fasciculus must be the key element of these tracts (Raïchline, 1900; Keraval, 1901).

Thus, Larionov, historically, belongs to a distinct group of authors who, through the study of clinical cases of aphasia, agraphia and amusia between the 1860s and the 1910s, documented that speech and language functions in the human brain are subserved by different systems than those of the musical faculty. Such authors included Jean-Baptiste Bouillaud, Armand Trousseau, Olof von Dalin, Adrien Proust, Edmond Brazier, Charles Féré, William Gowers, Gilbert Ballet, Johan Gustaf Edgren, José Ingenieros, and Otto Marburg (Johnson, Graziano, & Hayward, 2010; Koniari & Triarhou, 2010; Johnson et al., 2013). The preservation of musical abilities in cases with impaired speech was also noted by Hughlings Jackson, who referred to the ideas of Jules Falret concerning the ability of certain aphasic patients to produce words in singing that they cannot in speaking (Lorch & Greenblatt, 2015).

Hearing deficits in psychotic conditions

At the Fourth Congress of the Society of Russian Physicians in St. Petersburg in 1891, S. A. Belyakov presented a report of 12 cases in a lecture entitled, "The effect of the disease on the development of hearing and course of mental disorders." He detected an acute and chronic otitis with which he was trying to associate auditory hallucinations and an impaired sense of smell and taste. Additionally, in this lecture he introduced the term "hyperaesthesia acustica" or hyperacusia (Arkhangelsky, 1984).

It has been a long-known fact among psychiatrists that auditory hallucinations are often associated with subjective auditory sensations resulting from ear diseases. Aware of that, Larionov (1896) carried on the studies of Belyakov, by conducting detailed otorhinolaryngological examinations at the neuropsychiatric clinic of Bekhterev of 20 patients who suffered from various psychoses, including four patients with progressive paralysis. The hearing tests were conducted with the eyes closed, using tuning forks and a pocket watch. In most of them, Larionov detected a chronic catarrh of the Eustachian tube and the middle ear; five patients had obstructions from cerumen. Auditory hallucinations were reported by 12 of the patients. Larionov gave specific examples, such as of one patient who was hearing a constant cockcrow in the right ear, and another, whose head was occupied by a latent ghost of the national anthem. The hallucinations were contained or eliminated after the ear catarrh was managed. Based on the effective treatment outcomes in his material, Larionov emphasized the importance, in all psychoses, and especially in those accompanied by auditory hallucinations, of a detailed ear examination, diagnosis, and appropriate immediate treatment. He noted that the successful treatment of the ear condition, which is the source of auditory hallucinations, may often improve the mental state; in acute paranoia or hallucinatory confusion, elimination of the auditory hallucinations due to ear conditions might even lead to a rapid and complete disappearance of the psychotic symptoms (Larionov, 1899b; De Forestier, 1900).

Larionov discussed in particular two striking cases of severe psychosis and secondary mental retardation, which did not interfere with the musical perception and performing abilities of the brain. One of these patients could perform, promptly and with expression, the piano scores of demanding waltzes, mazurkas and other musical pieces, including a long Beethoven sonata. Thus, he backed his own work (Fig. 4), as well as the anatomical and physiological results of other researchers, on the localization of "a special musical sphere in the human brain" (Larionov, 1899b; Larionow, 1899a; De Forestier, 1900).

Other works

Larionov popularized the advances in the study of the structure and function of the auditory pathways in two monographs, one on hearing loss (Larionov, 1900), and the other on the psychology of verbal dexterity (Larionov, 1908). The latter was based on a lecture that he gave in St. Petersburg on March 4, 1907 (Table 2). He then decided to expand on his topic and describe the physiological and psychological bases of eloquence and the art of public speaking (Figs. 5, left, and 6, right). One cannot avoid noticing some early "Vygotskian" ideas, in that book, pertaining to the quintessential role of speech and language in the function of thought. The writing style is excellent; it attests a rounded education, as well as its author being abreast of developments in his field.

At the beginning of the 20th century, Larionov (Fig. 6, left) was one of the early physician-neurohistologists who gave detailed accounts of nerve endings in the cerebral cortex (Larionov, 1903a, 1905), along with Santiago Ramón y Cajal (1852–1934), the Russian cytologist Mikhail D. Lavdovsky (1846–1902), and Bekhterev (Shkolnik-Yarros, 1971). In 1905 Larionov gave a lecture before the Second Congress of Russian Psychiatrists in Kiev on the fine structure of the brain, the neuron theory, and individual brain centers (Larionoff, 1907; Larionov, 1907). In his presentation (Fig. 7, left), he summarized the data on the cerebral cortex already published by Meynert, Betz and Ramón y Cajal, and described the auditory cortex of dogs and its layer composition. He further reported on the cytoarchitecture of the inferior colliculus and its relation to the conduction of acoustic impulses

(Arkhangelsky, 1984). Larionov structured his presentation around three themes: the morphology of neurons and glial cells, the cellular structure of cortical centers (Fig. 8), and the projections of fiber pathways. Introducing his own modification of the Golgi method, Larionov examined the canine, feline, and human brain in coronal and sagittal sections (Fig. 9) and gave details on the histology of the grey and white matter of the cerebral hemispheres, as well as the pons, medulla, and cerebellum, with special reference to the substantia reticularis (later reticular formation) and its fiber bundles (Larionoff, 1907).

Here is a sampling from the conclusions in the paper on the associative centers of the brain (Fig. 6, left):

> In my view, consciousness and thought are representations of memories of the circumstances, events and subject matter of awareness, and do not represent by themselves anything supernatural; on the contrary, the revival or transformation of consciousness in the form of language is a much more complicated and impressive act of our mental life, the highest gift of the amazing human order. Thus, intelligent volitional speech constitutes a supreme psychological act, and thought and consciousness are only silent memories of experience…Lastly, it is impossible not to concur with Wundt's definition that psyche is "the inner existence of the entity that we call the body," which Leibniz calls "mirror of the world." It is not a mere entity, but a very complex product of development (Larionov, 1903a).

Larionov was especially proud of the successes of Russian neurology: in a review (Larionov, 1903b) he emphasized the importance of Bekhterev's neurological school and its key people who investigated the structure and function of auditory, gustatory and olfactory nervous pathways. He also reported on his own histological data indicating that a small part of nerve fibers originating in the canine auditory cortex descend to the anterior columns of the spinal cord, the cerebellum, and the cranial nuclei of the oculomotorius and the facialis.

Between 1903 and 1908 Larionov also became involved in studies on hysteria and neurasthenia and their neuropathological aspects. During his Odessa years, around 1913, Larionov, in collaboration with G. I. Kopytko, occupied himself with the problem of obesity and adiposis dolorosa, analyzing neuropathogenetic factors and insisting that the early treatment of obesity of diencephalic origin should be an absolute priority in national health care (Arkhangelsky, 1984).

In 1925 Larionov published a memoir recalling his and Bekhterev's early years in Kazan where the "Bekhterev school" was born. The latter's "Kazan period" began in the fall of 1885 and lasted through September 1893, when Bekhterev moved to St. Petersburg as director of the Clinic of Nervous and Mental Diseases of the Imperial Military-Medical Academy (Akimenko, 2007). Bekhterev had great personal charm and soon, "all the intellectuals in Kazan began to talk about him, especially his medical intellect, as a brilliant young scientist" (Larionov, 1925; Loginova, 2005). Larionov (1925) recalled: "Life is vigorous, so abundantly vigorous; the demands of the mind and the will rushed out to quickly transform into effort and to emerge in the form of scientific publications; Vladimir

Mikhailovich impressed everyone with his constant cheerfulness, joy of life, and most importantly, amazing capacity for work" (Loginova, 2005).

The following year, 71 Soviet and European scientists put together a *Festschrift* for Bekhterev on the occasion of the 40th anniversary of his first academic appointment in 1885 at Kazan University (Fig. 5, right). Larionov's chapter was a critical review of the state of knowledge on the vegetative nervous system and its pathology (Larionoff, 1926). He made the argument that, while the evolution of the nervous system has followed a course from lower to higher forms, its study by science has taken the reverse path, studying in detail the functions of higher centers and neglecting the vegetative nervous system, thus failing to penetrate deeply into elementary phylogenetic truths intimately linked to the affective sphere. He reviewed the progress that had been made over the preceding decade on the functions of the endocrine glands and internal secretion, as well as the observations on epidemic encephalitis that led to discoveries of complex aspects of the visceral brain. Such progress, he claimed, would benefit all medical branches, but especially internal medicine, neurology, and psychiatry (Fig. 7, right).

Discussion

Vladimir Efimovich Larionov deserves a place in the roster of the physician-researchers who contributed to the emergence of auditory cognitive neuroscience as a neurological discipline in its formative years during the late 19th and early 20th centuries. Larionov seems to have been one of those classically unrecognized figures of science. One of the aims of the present article is to remedy such an injustice. The research endeavors of the apprentice have deservedly emerged from the shadow of his celebrated master, Vladimir Mikhailovich Bekhterev. Larionov's innovative ideas opened up new ways of thinking in brain and behavior research. They probably have remained unheeded in the modern biomedical literature owing to their original publication in Russian and in German.

Larionov was highly regarded by his contemporaries (Arkhangelsky, 1984), including the electrophysiologist Vladimir V. Pravdich-Neminsky (1879–1925) of the Kiev school of physiology (Nemminski, 1913; Pouget, 2008). Eminent scientists in Europe and America recognized and acknowledged his contributions to brain research with reference to the neuroanatomy and neurophysiology of audition and the localization of musical centers in the brain.

Alfred Walter Campbell (1868–1937), who is known for presenting a system of parcellation into 14 cytoarchitectonic areas in his classic atlas and map of the human cerebral cortex, credited Larionov as "the first to have tried a novel and ingenious method of determining auditory localization, that is by obtaining galvanometric measurements of the current in the cortex of the temporal lobes during stimulation of the peripheral organs of hearing with tuning forks" (Campbell, 1905). Campbell (1905) summed up Larionov's contributions as follows: "In his published experiments on dogs, Larionov (1897c) combated Munk's statement that each center has a crossed connection with the contralateral side only, and holds that each ear is related to both cortical centers; he further finds that slight lesions of the auditory cortex are followed by a loss of appreciation of single tones without impairment of common hearing, and he has produced movements of both ears by faradization of the angular gyrus, as well as of the temporal lobe."

In Vienna, Richard Wallaschek reported Larionov's research (Wallaschek, 1900). In Italy, both Cesare Lombroso (1835–1909) and Giovanni Mingazzini (1859–1929) were familiar with it. Lombroso (1902) wrote: "According to Larionov, who also accepts the associative centers, the center for the perception of sounds in the dog would be in the posterior part of the brain, i.e., the part that, according to Vogt, becomes myelinated later; thus, it should be an associative center, according to Flechsig, albeit sensory." Mingazzini (1922) wrote: "Indeed, the assumption that in the posterior part of the corpus callosum commissural bundles connect the temporal gyri (or auditory centers) of the two hemispheres, as well as the occipital and the angular gyri of the two hemispheres, was confirmed by Turner and Ferrier in the monkey and by Larionov in the dog. Larionov, by destroying the auditory sphere of the temporal lobe on one side, traced the degeneration of the corresponding fibers through the corpus callosum up to the cortical auditory sphere of the contralateral side."

The renowned Eduard Hitzig (1839–1907) of Halle mentioned during the second Hughlings Jackson lecture, which he delivered before the Neurological Society of London on November 29, 1900: "Finally, within the last few months Larionov's experiments have taught us that this negative variation can also be traced in the reverse direction, insofar, namely, that the currents of cortical action experience a locally limited change when peripheric stimulus is applied" (Hitzig, 1900a); and "conversely, as shown during the last few months by Larionov, a negative variation occurred in a restricted area of the cortex after stimuli were applied to the periphery of the body" (Hitzig, 1900b).

The pioneer neurophysiologist Ivan S. Beritashvili (1884–1974) in Tiflis, Georgia acknowledged: "I may also cite the opinion of Munk that heterogeneous sounds have different cortical representations. Larionov in Bekhterev's laboratory tried to investigate this question in detail. By the extirpation of different areas of the auditory analyzer in the dog he succeeded in determining that musical sounds are represented in the cortex according to their pitch, i.e., the nearer the sounds stand to each other in the musical scale, the more closely do their respective cortical representations lie to one another" (Beritoff, 1924).

In the United States, Edith M. Brace (1890–1972) of the Biological Laboratory of the University of Rochester, New York, reviewed Larionov's experiments in dogs for the Publication Department of the Bausch and Lomb Optical Company (Brace, 1899). Years later, in a lecture before the Medical Section of the National Medical Association on August 19, 1941 in Chicago, the neuropsychiatrist Herbert J. Erwin (1912–1966) of the Homer G. Phillips Hospital in St. Louis, Missouri, credited Larionov for his studies in 1900 on the electrical cortical responses to various types of peripheral stimuli (Erwin, 1942).

The biophysicist N. A. Aladjalova of the U.S.S.R. Academy of Sciences credits Larionov for having been able to show that the frequent rhythmic stimulation of a cranial nerve may evoke an aperiodic shift of potential derived from the surface of the cerebral cortex. This is something that was also demonstrated some 60 years later with stimulation of the thalamic nuclei or the reticular formation, and is a phenomenon regarded as the result of the summation of trace processes (Aladjalova, 1964).

Bekhterev mentioned Larionov repeatedly in his voluminous textbooks (Bechterew, 1900, 1907, 1911). He amply credited Larionov and the localization studies in the auditory cortex in his own comprehensive reports on cortical function (Bechterew, 1899, 1926). Bekhterev summarized the discoveries of his pupil, highlighting his precedence in deciphering central nervous mechanisms, as follows (Arkhangelsky, 1984):

(a) Larionov was the first to establish the tonotopy center in the auditory cortex.

(b) He formulated the hypothesis that the center of music perception is located in the lowest compartment of the insula (central gyrus), in proximity to the vocal center behind Broca's area.

(c) He was the first to describe the descending (i.e. efferent) fibers from the temporal auditory cortex to the superior corpora quadrigemina in the posterior commissure, as passing through the posterior part of the internal capsule to the inner epithalamic commissure and from the latter to the inferior colliculi, with some fibers projecting to the dorsolateral thalamus through the stratum zonale.

(d) He established the connection of the fourth outer gyrus and the olfactory lobe with taste perception.

(e) He was the first to suggest that the right frontal center subserves affective behavior, i.e., an evaluation of the pleasant and the unpleasant.

Summary

In the present study we highlighted an important aspect of the history of auditory neuroscience, by reviewing the relevance of the work of V. E. Larionov, which would otherwise have remained largely neglected to contemporary scholars; we attempted to describe a crucial historical, scientific and geopolitical context in the progress of neurophysiology and neuroscience in general.

Information on the life of Larionov has been fragmentary. The turning points of his career were recorded by G. V. Arkhangelsky (1984), a neurologist and medical historian. Larionov's captivating writing style and subtle personal comments allowed us to portray him through his works.

Having attended a topmost gymnasium and university in Imperial Russia, Larionov emerges as a person with a comprehensive background. He chose the career of a military physician in combination with experimental and clinical research and teaching. One appreciates his meticulousness, attention to detail and perseverance in advancing any project to the highest level, be it the tracing of degenerating fibers using serial sections or the detailing of acoustic cortical maps using tuning forks. With his ideas and precise experiments, Larionov changed some traditional views.

A musical mastery also becomes evident, with undeniable analytical skills regarding the construction of the violin. His broad erudition and diverse skills interrelated in multiple fields, and his writing talent was not an exception. Each of his publications reflects the analytical mind, being well structured and comprising exhaustive historical excursus with minutiae and vivid examples. The flow of his writing is rhythmic, passionate, harmoniously bringing together form and essence, and ultimately revealing a genuine nature.

Larionov's personality is particularly perceptible in the "Psychology of eloquence." He recalls how he used to repeat fragments from the speeches of Demosthenes while walking to work during his Kiev years. In listing the qualities that a true speaker should possess, Larionov describes the requirements set to his own self:

> One should grow as comprehensively as possible, read the classics in his field and in the literature in general in order to produce a concise and figurative language and learn the elegant touch of style and rhythmic syllables…Only speech coming from the heart, genuine and cherished in the depths of the soul, captures listeners. Only inner conviction and judgement can provide the speaker with force and confidence. Lastly, one must have the strength of will to express one's speech with vigor and energy that will transmit the confidence about everything enunciated to the listeners (Larionov, 1908).

Larionov lived around the *fin-du-siècle*, but not simply from the viewpoint of timeline. His emergence as a gifted researcher coincided with the development of clinical and theoretical neuropsychology in Russia, as the young Bekhterev was embarking in 1885 on his meteoric scientific rise at Kazan University. In his mature age, Larionov had to live through the complex transition to the different political era of the country, not emigrating, but loyal to his vocation.

Based on the list of his papers, we see that, one way or another, V. E. Larionov remained connected to Bekhterev through the years. He was repeatedly invited, as a colleague, to contribute to the Bekhterev homage compilations, even in 1925, while practicing otorhinolaryngology in Odessa. This appears to be his last known publication, a review of the phylogenetic, structural and functional aspects of the autonomic nervous system and the diagnostic and practical aspects of related pathologies, witnessing, once more, the comprehensive style and approach of the master of a great physiological school.

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Figure captions

Fig. 1. *Upper:* Vladimir M. Bekhterev, in the center, among his closest colleagues in the Department of Psychiatry at Kazan University. Photo from the introductory matter in the 40-year Bekhterev *Festschrift* (cf. Larionoff, 1926). *Lower:* The Imperial Military-Medical Academy of St. Petersburg, circa 1895–1900. (Credit: Library of Congress).

Fig. 2. *Left:* The title page of Larionov's 1898 doctoral dissertation (Larionov, 1898e). The handwritten inscription on the top right reads: "To the respected Vyacheslav Pavlovich from the author for the good memories." In the acknowledgments, on page 368, Larionov wrote: "I consider it my duty to express my deep and sincere gratitude to Professor V. M. Bekhterev for the suggestion of the topic and for his guidance in the execution of this work. I am equally thankful to Professor N. P. Simanovsky and his assistant B. V. Verkhovsky." (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited. *Right:* The cover of Larionov's monograph on the acoustic secrets of old Italian violins (Larionov, 1910a); the address (work or domicile?) shown is 5 Lermontovsky Lane, flat 6, Odessa. (Courtesy: The V. I. Vernadsky Library of The National Academy of Sciences of Ukraine, Kiev; catalog record 31115).

Fig. 3. The *top* scheme shows an 85-key piano keyboard with the octave names (in English and in German) conventionally used in music theory. The notes of eleven tunings forks that Larionov used in his experiments are depicted with gray circles on one flat and ten natural keys, along with their corresponding audio frequencies according to Helmholz (Larionov, 1898e; Bechterew, 1911). [In Central European notation, *h* is used for natural Si and *b* for Si-flat.] Just below them, the three zones into which Larionov divided the canine (and homologous human) temporal cortex are denoted in modern neuroanatomical terminology; lower notes were represented caudally and higher pitches rostrally in the temporal gyri. The *lower* composite shows brain drawings from Larionov's doctoral dissertation (Larionov, 1898e), except for brain 3, redrawn by Bekhterev (Bechterew, 1911). *Brain 1:* Functional localization in the cerebral cortex of the dog as described by Munk (1881) based on experimental lesions, redrawn by Larionov; *B*, auditory cortex *(Hörsphäre). Brain 2:* A drawing of the canine brain by Larionov, borrowed from Professor Benno Baginsky (1848–1919) of Berlin, with modern neuroanatomical terms superimposed for the sake of the present discussion. *Brain 3:* Larionov's results summarized by Bekhterev in a general scheme of pitch reflexes in the temporal region (Bechterew, 1911). *Brains 4 and 5:* Experiments 1 and 5 of Larionov, with three temporal gyri surgically removed as a transverse strip. *Brain 6:* The original "functional map" of pitch localization in the cortical auditory areas of the canine brain as deduced by Larionov; lesions placed at different points along the S-shaped trajectory resulted in failure to respond to pitches of different frequencies. *Brains 7 and 8:* Drawings of human cerebral hemisphere from Larionov's thesis (Larionov, 1898e), depicting the insula *(Ostrovok)*, Wernicke's area, and the tone center *(Tonovoy tsentr). Brain 9:* Similar to 8, from Larionov's sequel paper in German (Larionow, 1899a). [A note on comparative anatomy: The caudal one-third (or one-fourth) of the canine suprasylvian gyrus corresponds to the middle temporal gyrus of humans, the caudal one-third of the canine ectosylvian gyrus to the superior temporal gyrus of humans, and the caudal one-half of the canine perisylvian or angular gyrus to the postcentral insular

area of humans. The part corresponding to the canine angular gyrus in humans, the insula of Reil, is concealed by the marked growth of the frontal and temporoparietal gyri, or anterior and posterior associative centers of Flechsig.] (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited.

Fig. 4. *Left:* "On the musical centers of the brain." Frontispiece of Larionov's paper in German (Larionow, 1899a). *Right:* The first premises of Bekhterev's Psycho-Neurological Institute in the commercial buidling at 104 Nevsky Prospekt, St. Petersburg, circa 1908. Photo from the introductory matter in the 40-year Bekhterev *Festschrift* (cf. Larionoff, 1926).

Fig. 5. *Left:* Cover of Larionov's monograph on the "Psychology of eloquence" (Larionov, 1908). *Right:* Frontispiece of the *Festschrift* compiled on the occasion of the quadragennial of Bekhterev's first professorship at Kazan University (cf. Larionoff, 1926); the list of contributors from countries other than the Soviet Union included such distinguished scientists as Édouard Claparède (1873–1940) of Geneva, Edward Flatau (1868–1932) of Warsaw, Karl Kleist (1879–1960) of Frankfurt am Main, Giovanni Mingazzini (1859–1929) of Rome, Otto Marburg (1874–1948) of Vienna, and Stjepan Poljak (1889–1955) of Zagreb. Chapters were published in Russian, German or French. (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited.

Fig. 6. *Left:* Functional localization diagram of the human cerebral hemispheres drawn by Larionov (1903a). In the left hemisphere, from the frontal to the occipital pole (top to bottom in the figure) the drawing sequentially depicts: the center of abstract notions or ideas (anterior shaded area); center of volition or will in the form of desires, decisions and conscious movements; Broca's area and motor center of writing; motor centers; unconscious repetition of words and vocalization area of Krause; musical center; Wernicke's area; center of awareness; tactile notions; center of word memory; visual center of writing; visual occipital area. In the right hemisphere, in the same direction, the drawing depicts: the center of affective ideas and emotional awareness; volitional center of the so-called free will; motor centers; center of subjective notions or "mind" (posterior shaded area); visual occipital area. Abbreviations: *i*, hearing; *к*, vision; *i* to *a*, conscious repetition of heard words, and path of speech development; *к* to *б*, conscious reading; *в*, conscious volitional speech; impulses go from word memory center, which is enhanced by the volition center; *i* to *г*, subconscious repetition of words (reflex speech): primary path of speech development; *д*, affective speech; *к* to *е*, reasoning/conscious writing/copying; *к* to *ж*, subconscious (automated) writing/copying; impulses to conscious writing originate from the visual center of writing and travel via path *е*; *з*, conscious volitional acts; *и*, affective acts. (Courtesy: The V. I. Vernadsky Library of The National Academy of Sciences of Ukraine, Kiev; catalog record 31116). *Right:* A synthetic drawing by Larionov (1908) of the anatomical centers and connections for speech, language and consciousness, from the "Psychology of eloquence." Abbreviations: *а*, major cerebral sulci. Centers, paths and organs of phonation: *А*, higher motor center of phonation or singing of Fedor Krause; *Б*, lower motor center of phonation of the inferior colliculi of Bekhterev; *В*, motor-sensory nucleus of vagus extending to muscles of larynx; *Г*, main organ of phonation, the larungeal muscles and glottis; *Д*, Broca's motor speech area; *Е*, thalamus; *Ж*, motor nucleus of hypoglossal nerve extending to the tongue *И*, the main organ of articulation and

speech; it also connected through the other centers to the nucleus of the hypoglossal nerve *Я. 3*, lower center of facial nerve innervating the muscles of the lips and face *i* for performing partially articulation and partially mimic movements; *K*, ear; *Л*, primary lower auditory centers of medulla oblongata; *M*, auditory center of inferior colliculi; *H*, higher auditory cerebral organ for pitch perception; *O*, Wernicke's speech perception area (destruction of *Л*, *M* and *O* may lead to amusia or speech and verbal deafness; disruption of the lower speech arch leads to paraphasia, while disruption of the higher speech arch at *O-Ф* or $У^1$-*Д* leads to sensory or motor transcortical or psychic aphasia, respectively). Organ of vision, its centers and paths: *Ш*, eye connected by the optic nerve to the lower visual center of the superior colliculi *Ю*, and the respective higher center of the cerebral hemispheres; *P*, visual associative or psychic center of writing and reading, center of memories of written signs and their visual symbols (its destruction leads to sensory agraphia and motor alexia, i.e. the patient cannot write and read because he does not remember any written symbols); it is connected with the general visual center *П*, Wernicke's area *O*, the associative or psychic center of auditory memory for words *Ф* (its destruction leads to amnesia), the tactile center *X*, the motor center of writing *C* (its lesion leads to motor agraphia), and also to Broca's area *Д*, which is not shown in order not to confound it. *У-У-У*, posterior associative or psychic center, capturing and combining (associating) all sensory sensations—tone, speech, auditory, visual, tactile, gustatory and olfactory—via the special designated, within it, centers of memory for each sensation, as, for example, center of written impressions or memory of written characters *P*, center of auditory memory of words *Ф*, center of tactile impressions or tactile memory *X*, etc. This center combines the specific subjective notions or visual, auditory, and other memory; it associates impressions of the outside world; its damage causes loss of memory of the objective visual and other notions and of the auditory memory of words that define subjects (nouns and proper nouns). $У^1$-$У^1$-$У^1$-$У^1$, anterior associative or psychic center combining our motor and other internal affective, emotional, visceral and bodily feelings belonging to internal abstract thinking; it associates mutual sensations of abstract notions and the various expressed qualities of feelings and acts of movement and action; its damage causes memory loss of adjectives defining different qualities of subjects and general human feelings, as well as memory loss of verbs that define human actions; its damage leads to an impairment of the primary, higher, subjective, critical, sensory, volitional and acting human personality combining images from the inner world; similarly, damage of the previous associative center leads to suffering of the secondary lower objective personality that combines impressions from the outside world; these impressions or imprints of different memories, revived by consciousness and attention, become notions or ideational concepts for the first associative center. Both of these centers are connected to each other for the revival of the memory of specific subjective and abstract notions in consciousness and for associating them with each other. Consciousness and attention have to be allied to the first associative center, i.e. to the primary personality, according to the opinion of S. I. Chirev, closely connected with the fornix, and semi-consciousness or subconscious psychical activity of the secondary personality, expressed, for example, during sleep, hypnosis, as well as in psychiatric patients, which must be attributed to the posterior associative center. (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited.

Fig. 7. *Left:* Frontispiece of Larionov's paper, in German, on the fine structure and a new staining method (Golgi modification) of the human and animal brain (Larionoff, 1907). *Right:* A summary, in French, of Larionov's review on the vegetative nervous system and its pathology, appearing in the Bekhterev "Festschrift" (Larionoff,

1926). (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited.

Fig. 8. Drawings by Larionov from actual microscopic preparations processed with his own modification of the Golgi method (Larionoff, 1907). Anterior one-third and anterior one-half of the human middle frontal gyrus, left cerebral hemisphere; drawings artistically supplemented with colors by Larionov for the sake of clarity of the cell groups and processes. Zeiss DD objective (numerical aperture 0.82, air angle 110°, equivalent focal length 4.3mm, magnification ×175 to ×580, depending on eyepiece). *Abbreviations: Pia*, pia mater; *v*, blood vessels; *kfz*, jug-shaped cells; *k*, axis cylinders; *p*, pyramidal cells; *ws*, white matter; *gM*, ganglionic mass; *gz*, glial cells; *sz*, radial cells. (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited.

Fig. 9. Drawings by Larionov from preparations processed with his own modification of the Golgi method (Larionoff, 1907). Drawing 5: Coronal section through the central gyri of the dog brain. Drawing 6: Coronal section through the upper half of the left cerebral hemisphere of the dog brain behind the central gyri. Drawing 7: Coronal section through the superior frontal gyrus of the human cerebral hemisphere, showing a mulberry in the area of the central gyri. Drawing 8: Sagittal section through the cat brain. Natural size. Drawing 5–8: natural coloration, as seen in the histological specimens. Drawings 5–7: Zeiss AA objective (numerical aperture 0.31, air angle 36°, equivalent focal length 18mm, magnifications ×38 to ×130, depending on eyepiece). *Abbreviations: p* and *pz*, pyramidal cells; *ws*, white matter; *gM*, ganglionic mass; *gz*, glial cells; *sz*, star-shaped cells; *cz*, colossal cells; *kp*, small pyramidal cells; *gp*, large pyramidal cells; *pp*, fiber plate from the region of the optic thalamus; *to*, optic thalamus; *nc*, caudate nucleus; *sr*, substantia reticularis; *M*, mulberries; *czv*, colossal cells in vacuoles; *ci*, internal capsule; *cc*, corpus callosum; *vl*, lateral ventricle; *gc*, central gyrus; *gcn*, cingulate gyrus; *gp*, parietal gyrus; *nl*, lenticular nucleus; *aF*, association fibers. (Authors' private archive). Copying, redistribution or retransmission without the authors' express written permission is prohibited.

Table 1 — The conclusions from the doctoral dissertation of Larionov (1898e), rendered into English from the old Russian text.

In closing, we must draw the following conclusions from this work:

1.—Upon partial destruction of the cortical temporal gyrus in dogs, partial deafness to certain pitches occurs.

2.—The temporal portion of the second outer gyrus contains centers for the pitches of the lower octaves from E to A_1 and lower; the temporal compartment of the third gyrus contains centers for the pitches of the middle octaves from E to C_2; and the posterior one-half of the fourth gyrus contains centers for the pitches of the high octaves, from C_2 and higher.

3.—A pitch scale which corresponds to the pitch scale of the cochlea of the ear exists in the temporal cerebral lobe.

4.—Each pitch center, apparently consisting of a group of cells, is connected via fibers with a group of hair cells in the organ of Corti and corresponds to a group of similarly tuned strings of the basic membrane, approximately by the octave.

5.—The response to sounds descends in parallel with the response to pitches, such that sounds are perceived by the tone scale.

6.—After minor destruction of the temporal cortical region, eventually almost full tone deafness occurs, frequently owing to degeneration of the association, commissural and projection auditory pathways in the cerebral hemispheres and the midbrain bilaterally.

7.—The remaining weak hearing response depends on the auditory centers of the inferior colliculus.

8.—Faradic current stimulation of the cortex of all three temporal gyri provokes the ears, the eyes and the head, or the so-called cortical reflex, similar to the primary auditory reflex, dependent on the inferior colliculus.

9.—Munk's psychic deafness does not occur in the destroyed central field of the auditory cortical areas (perhaps it is associated with the destruction of the posterior associative centers of Flechsig).

10.—Based on the data in the literature on amusia and verbal deafness from Edgren and from experimental data, we must admit, particularly in the case of amusia, the complete independence of Wernicke's area from the tone or musical center, as individual pathways exist for each. Wernicke's area is located in the first temporal gyrus, superior and posterior to the tone center, in the region of its middle octaves, namely, in the region of notes B_1–G_1. In dogs, Wernicke's area is possibly in a primordial stage because many animals perceive, understand and remember words; nonetheless, the tone center is well developed.

11.—Wernicke's area subserves the perception of words, but it does not represent the center of verbal image memories, which is possibly subserved by the posterior associative center of Flechsig; this is established from the cases of transcortical aphasia, particularly the classical cases of Heubner.

12.—Upon destruction of Wernicke's area, verbal deafness occurs, but there is not a mnemonic loss of verbal images.

13.—The tone and musical center in humans is possibly consistent with that in dogs; it is necessary to assume that the centers of low pitches, in the sequence of their scale, are located in the anterior one-half of the human middle temporal gyrus, the centers of middle pitches in the anterior one-half of the superior temporal gyrus, which corresponds to the third gyrus of dogs (rostrally to Wernicke's area), and the centers of high pitches are located in the posterior gyri of the insula, which corresponds to the fourth (angular) gyrus of dogs.

Table 2 — Excerpts from the book by Larionov (1908) on the "Psychology of eloquence" (Figs. 5, left, and 6, right), freely translated from the old Russian text to convey some key ideas.

Eloquence is the supreme gift that only nature could give to humans; this is why it is a subject of interest in all cultured nations. Even in ancient Greece and Rome, orators were deservedly honored. Any intellectual person knows famous speakers like Demosthenes, Cicero, and the French human rights activist Gambetta.

The topic has great scientific and practical meaning. There is nothing that can reveal psychological problems or challenges as the principles of speech and eloquence, and there is nothing as important for practical human life…Therefore, it is not without reason that speech is considered a great instrument of the mental development of humans. In science, the ability for speech includes a so-called inner language, which comprises the writing ability.

In ancient Greece and Rome, along with classical literature, educated people possessed an ability for, and paid a lot of attention to, the gift of speech. Since then, humanity descended to the development of written language, and only in England, thanks to the Parliament (from 1300 on) one could "speak." In ancient Greece, there were no defenders in court, and there was a ritual—plaintiffs or defendants had to speak themselves, for which they were pre-trained by orators who knew all the rules of the art of speaking. Besides, speeches were uttered, for example in Athens, anywhere people gathered. In ancient Rome, writers in the Senate only numbered ten…

Any subject is unknown to us by its meaning; we only know its features, not the essence. The same concept applies to the forces of nature…Let us take a closer look at what eloquence is from a psychological perspective. At first impression, the question is not as simple as it may seem. The cause is hidden in the secrets of the brain. To understand and comprehend it, it is necessary to learn what speech is and what the psyche is, and of what components they are composed.

There is a science of speech disorders, the science of aphasia, which represents a collection of precise experiments by nature over man—experiments that cannot be conducted artificially: they provide psychology with rich material that is impossible to compare with psychological experiments and allow us to discover the essence of speech. It turns out that speech is the most complex and highest mental ability. It is the mirror of the psyche, as it represents all our sensations, feelings, understandings, ideas and thoughts in verbal images.

The development of the ability to speak is also very complex. Speech is composed of vocalization (or phonation) and clear pronunciation (or articulation). The mental development of the child begins with hearing, which is the most potent sense in human speech and mind development. It is followed, in significance, by developing the sense of vision. These two senses play the most important role in developing our psyche, because the association of their images is a basis of mental development overall. From these sensory images, first by reflex and then by both reflex and consciously, motor acts of speech and writing develop involuntarily. The other senses play a less important role in this respect. Consciousness here plays a secondary role as an intermediate addition to our enormous subconscious sphere of senses and movements…A constant purely imitative reflex training of speech skills, facial expressions and emotional feelings by the mother continues up to the fifth or sixth year of the child.

Eloquence is the ability not only to speak speedily, but to speak well: intelligently, freely, smoothly, expressively. Eloquence is due to the ability to correctly, freely and relatively quickly revive the visual, auditory and other sensory images and ideas and to consciously illuminate them. But of utmost importance it is to obtain free motor impulses for transforming images into freely articulated speech. The revival of sensory, ideational and motor images is called *internal speech*, and their externalization via motor impulses, *external speech*.

From the psychological perspective, there are classes of orators, based on the production of internal speech. There are orators called *movers*, who, when thinking, pronounce the entire speech quietly using the tongue and lips—representatives of Broca's area. They speak and listen to themselves. Gambetta was of that type. It is accustomed to consider them the best orators, but this is not entirely true. Other orators are the *listeners*; they hear the speech by the internal hearing and then as if repeating the internal words. The third type, the *viewers*, see each word of written speech and then as if reading the speech. This is why they must first write the speech down. But there are also *indifferent* orators, whose words, images and ideas pour out of the sphere of subconscious flow, such that the attention of consciousness, rational criticism and the will keep them in a fine line and direct speech to the logical path of thought. I belong to this type of people. I call them indifferent orators, i.e. reviving words as images of ideas. They possess a richer memory for ideas compared to the memory for subjects and names; this is why they sometimes forget words and names, and therefore have to take notes of some phrases and names to compose the speech plan. Their temporary word forgetting is due to their abstract thinking and richness of ideas which overpower the names of subjects and people.

The above defined orator qualities again prove that the subconscious sphere plays a huge role in the psyche and in our speech and oratorical mental activity. The highest mental component, *consciousness*, plays here a secondary role, although, of course, it is important for the speaker that the mind strictly monitors and guides the unconscious sphere, otherwise one will utter excess.

There are many factors that influence speech, including education, environment, health, psychological type, habits, temperament, character and will power. Such a diversity of factors and their interaction produce a variety of speaker types. If one is accustomed to speaking since early childhood, one will keep that ability as an adult.

What needs to be done to become an eloquent orator? A true orator has to learn coping with the enormous material that the subconscious sphere presents him with, to deliberately and skillfully draw everything necessary for speech making in agreement with the voice, feeling, breath, audience, etc. And those who cannot, should practice getting deeper into ways of their own thinking and speaking more frequently. This helps to bring all the memories of the more vivid images and makes it easier to run their thoughts and phrases. Cicero and Demosthenes are examples that prove what hard work can do.