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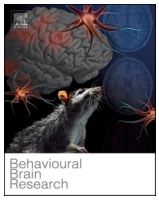

The Suok 'ropewalking' test of rodent anxiety and sensorimotor disintegration: A 20-year summary of its application in neuroscience research

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ABSTRACT

The Suok (ropewalking) test has been developed in 2004 to simultaneously assess rodent locomotor activity, anxiety-like behavior, sensorimotor disintegration, and their interplay. Over the last 20 years, this 'hybrid' test has been used in rat and mouse neurobehavioral research by various laboratories globally. Here, we provide a detailed overview of the Suok test, its past and present uses, methodological strengths, limitations, the existing problems, potential future modifications and practical applications. We also discuss the implications of results obtained in this test for improving our understanding of brain pathogenesis and the development of therapies for anxiety, vestibular disorders, sensorimotor disintegration and its stress-induced subtype. Finally, we suggest novel potential avenues for adapting this behavioral paradigm to the current needs and challenges of rodent preclinical neuroscience and drug discovery research.

1. Introduction

Animal models are a valuable tool in neuroscience research and are increasingly utilized for central nervous system (CNS) drug discovery [1,2]. Introduced 20 years ago [3,4], the Suok 'ropewalking' test that simultaneously assesses rodent anxiety, motor activity, sensorimotor disintegration (SD) and stress-induced sensorimotor disintegration (SSD, Fig. 1), is presently widely used in various laboratories worldwide [5–8]. Over the years, it has become an established, sensitive and efficient protocol for neurobehavioral stress research, including modeling stress-induced conditions, pharmacological modulation of anxiety levels, as well as behavioral phenotyping of genetically modified animals [9,10]. Other useful applications of the Suok test include studying neurodegenerative [11] and neurological (e.g., vestibular) disorders [12], consequences of exposure to toxins [13], burns [14] and traumatic brain injuries [12], modelling atherosclerosis [15], and testing the effects of various CNS drugs, such as anxiolytics [16] and sedatives [7], as well as various herbal extracts [5,17–21].

The test, originally developed in 2004 in the Medical School of the University of Tampere (Finland) was named after a tightrope-walking character in the classical 1927 Yuriy Olesha's novel "The Three Fat Men" [3]. The rodent Suok test was specifically designed as a fast, easy-to-perform 'hybrid' behavioral assay to assess simultaneously several domains, such as locomotor, anxiety-related behavior, vestibular impairments, their interaction, motor disturbances and SD [3,4,22]. However, although 20 years passed since its introduction, there have been no systematic analyses of the present and past uses of the Suok test, the existing challenges, and its future applications. Addressing this

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knowledge gap, here we provide a detailed updated overview of the Suok test's methodological strengths and limitations, its uses in research, and broader implications of results obtained in this test for the development of pharmacological agents aimed at treating anxiety, vestibular disorders, and SD.

2. The regular and the light-dark Suok tests

The standard Suok test apparatus for mice consists of a 2–3-m metal (e.g., aluminum or steel) rod 2 cm in diameter raised to a height of 20 cm above the floor [3,10] (Fig. 1), segmented into 10-cm sections and mounted on two Plexiglas side walls (e.g., 50 × 50 cm; 1 cm thick) to prevent rodents from escaping the experiment setup sideways. The rat Suok test modification includes a white aluminum or wooden alley (240 cm × 5 cm × 1 cm) divided into 15-cm segments and raised to a height of 20 cm with two vertical supports (with or without Plexiglas side walls) [4]. The floor beneath the setups is typically covered with a thick layer of bedding or other soft material, to serve as a cushion because animals can fall or, occasionally, jump off the rod [17] (Fig. 1).

In the regular Suok test, the experimental room is uniformly illuminated, and is usually dimly lit during the procedure to reduce stress and anxiety in the animals being tested, since overly bright lights can alter their behavior, potentially skewing results related to anxiety. During the test, the animal behaviors (Figs. 2 and 3) are typically recorded for 5–10 min by an experienced observer and/or video camera [4]. Throughout the observation, the experimenter is usually located in a nearby room or positioned/seated still near (e.g., approximately 2 m in front of) the apparatus, recording anxiety-related behaviors, motor activity, and (in case of animals falling) placing them back in the same position [23]. Since anxiety typically reduces animal exploratory activity [24], the horizontal, vertical, and directed exploratory activity is generally lower in anxious animals in this test [23].

Another key modification of the test is the light-dark Suok test (LDST, Fig. 1 inset), inspired by the light-dark box anxiety test [25,26]. LDST is typically performed in a dark room with a brightly lit 'aversive' area covering one half of the rod or alley (serving as an additional anxiogenic factor), whereas another half remains dark and is preferred by rodents as 'protective', evoking less anxiety [23]. The LDST uses the same apparatus as the regular Suok test, but with directed illumination of the light half of the apparatus provided by several bright 60-watt bulbs positioned above the test (e.g., at a height of 40 cm, Fig. 1) [3].

Enabling modelling anxiety-like behavior in a way similar to the traditional open field test, novelty exposure is the main feature of both Suok test versions, based on reduced exploration of a novel rod (mice) or alley (rats) arenas, as well as increased freezing behavior and vegetative indices (e.g., urinations and defecation boli) [3,4]. However, beyond reduced exploratory behavior, anxiety-like states frequently co-occur with additional behavioral alterations, such as SD [27]. Sensorimotor integration helps the brain combine sensory information from various inputs, and is critical for coordinated execution of motor programs [28]. In contrast, impaired integration of sensory inputs causes aberrant processing of motor programs in the motor cortex and may play an important role in the symptomatology of some other key disorders, such as Parkinson's and Huntington's diseases, as well as focal dystonia [29].

Stress strongly impacts the interactions between subcortical (e.g., limbic) and cortical areas (e.g., the prefrontal cortex), with the amygdala playing a crucial role in threat detection and generating emotional responses, and the prefrontal cortex being essential for higher-order cognitive functions and the regulation of emotions [30]. Disruptions in the functional balance between these regions can result in SD, as the brain becomes unable to effectively integrate sensory information with motor planning [31,32]. SD results in distorted perception of body and spatial relationships, sometimes leading to spatial disorientation and subsequent anxiety, as clinical patients with anxiety disorders display dizziness, nausea, misjudgment of distances to objects, fear of falling and illusions of movement in space [33]. Additionally, some anxiety disorders, such as agoraphobia, acrophobia/cosmophobia, panic attacks, and obsessive-compulsive disorder (OCD), are characterized by the simultaneous presence of anxiety and disturbances in spatial perception [34,35]. Furthermore, in various clinical experiments, participants with high

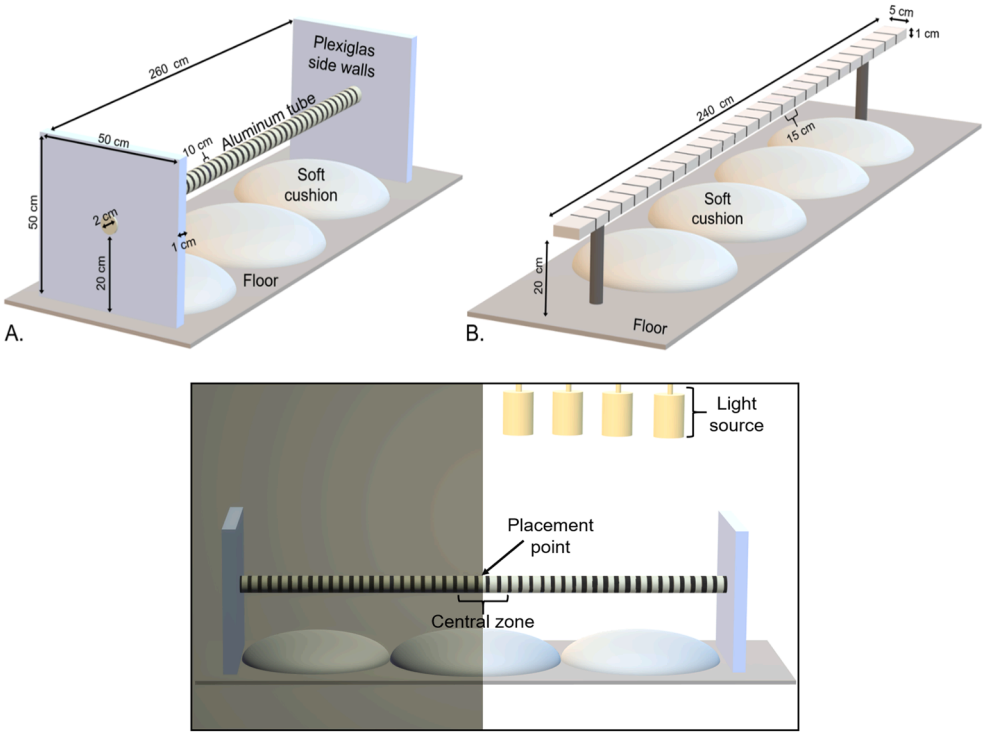

Fig. 1. A general illustration of the mouse (A) and the rat (B) Suok test apparatuses, as well as the light-dark modification of this test (LDST, bottom inset), according to the protocol for using the Suok test [3,23]. Note cushion pads placed at the bottom of the test, to minimize harm to animals.

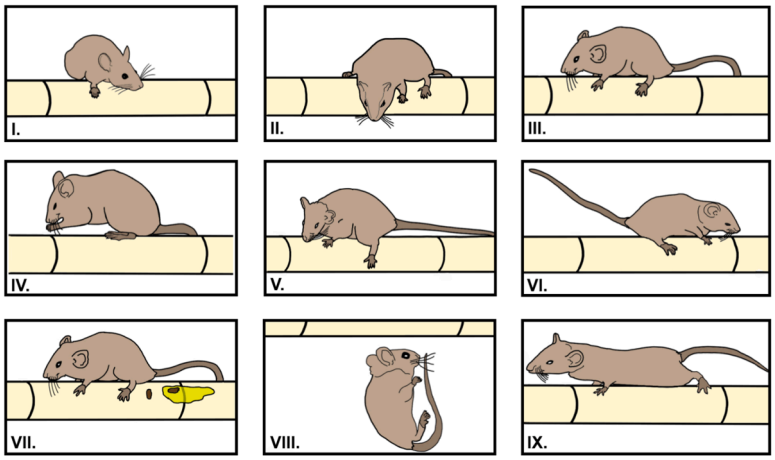

Fig. 2. An ethogram of typical mouse behaviors in the Suok test: (I) side looks, (II) head dips, (III) freezing, (IV) self-grooming, (V) hind leg slips, (VI) 'anxious tail' position, (VII) defecation/urination, (VIII) falls, and (IX) stretch-attend postures, according to the protocol for using the Suok test in mice [23]. Note that mice, albeit infrequently, can also actively jump from the rod (not shown).

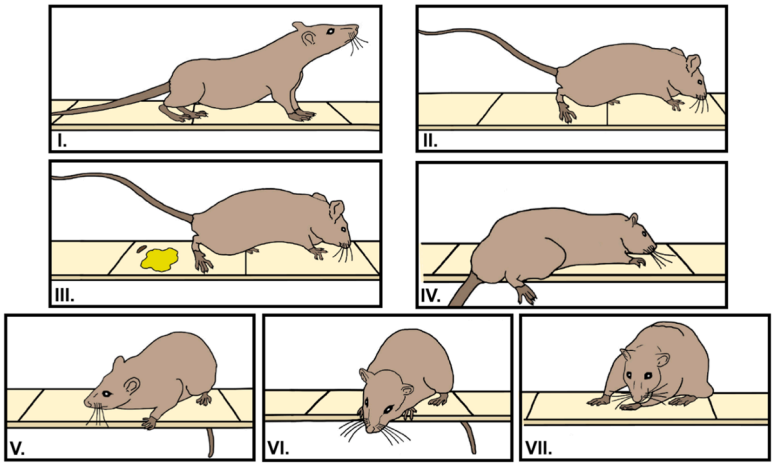

Fig. 3. An ethogram of typical rat behaviors in the Suok test: (I) stretch-attend posture, (II) horizontal locomotion, (III) defecation/urination, (IV) hind leg slips, (V) side directed exploration, VI) head dips, (VII) exploratory side looks, according to the protocol for using the Suok test in rats [23] (self-grooming is not shown). Note a general similarity of these phenotypes with those seen in mouse version of this test (Fig. 2). Also note that like mice, rats (albeit infrequently), can also actively jump from the alley during the trial (not shown).

anxiety perform worse on sensorimotor tasks, lose balance more frequently, and rely predominantly on one sensory input (i.e., vision or proprioception), demonstrating SD [36–38]. Thus, when complete integration of sensory information is not possible due to visual impairment, anxiety symptoms often emerge, along with balance disturbances due to the strong influence of visual input on postural control [39].

3. Translational relevance and experimental applications of the Suok test

High prevalence of clinical anxiety and related emotional disorders, as well as neurological (e.g., coordination and balance) deficits, and their comorbidity [40], calls for further in-depth studies in both clinical and experimental (animal) models [41], especially rodents [42,43]. For example, they display similar anxiety-related CNS processes with humans, including amygdala activation and hypoactivity of the anterior cingulate cortex [44], stress-induced hyperthermia [45], startle- [46], neuroendocrine [47] and vegetative responses [48], and the reduction of anxiety symptoms after treatment with anxiolytics [43] and chronic antidepressants [49]. These similarities allow for a detailed study of pathological mechanisms of anxiety and the development of new approaches and drugs for the treatment of anxiety disorders.

Using murine models holds significant importance for studying SD due to their manifested sensitivity to conventional anxiety markers and balance control proficiency. For example, BALB/cByJ mice, known for their heightened anxiety levels, display higher susceptibility to falling in the rotating beam test and poorer performance in the rotating tunnel test than less anxious C57BL6/J mice who exhibit enhanced balance maintenance during these assessments [50,51]. A parallel link between the vestibular system and stress/anxiety can also be observed in rats, as subjects with gentamicin-induced balance impairments cover less distance, take less time to enter the center of the open field test, dwell less time in the open arm of the elevated plus maze, and show elevated brain monoamines (as markers of heightened anxiety) than controls [52].

However, despite the wide range of tests available for identifying anxiety and vestibular dysfunctions separately [53,54], there is a clear lack of protocols that target the real-time interaction between these two states. Thus, the development of the Suok test and its modifications was timely to specifically fill this gap by directly and simultaneously assessing rodent stress and sensorimotor deficits, hence adding a new (i.e., SD-) dimension to the existing behavioral tests. In general, SSD can be modelled experimentally, for example, exposing mice to rats as predator, and counting falls and slips of hind limbs as SD markers in the Suok test [3]. Prenatal exposure to toxic substances also induces SD in adult

animals, and can be analyzed in the Suok test [7,8,55]. For example, the Gulf War Illness (GWI) is a complex chronic disorder affecting veterans of the 1990–1991 Gulf War, marked by a diverse array of symptoms difficult to diagnose and treat [56]. Modelling GWI in rodents involves a 5-min restraint stress and the administration of a combination of toxic substances utilized during the Gulf War, including the insecticide permethrin, the insect repellent N,N-diethyl-meta-toluamide, and pyridostigmine bromide. The impact of GWI toxins on sensorimotor integration and anxiety in mice in two studies using the Suok test includes elevated anxiety-like behavior (evidenced by reduced exploratory side looks and head dips) and more urinations and defecation boli [13]. Furthermore, altered sensorimotor integration is also observed in these mice, as evidenced by an increased number of segments crossed during the test [13,57].

Importantly, the interplay between anxiety and balance has specific neuronal substrates in the brain. For example, sensory information from vestibular nuclei and cerebellum, as well as afferent visceral and somatic information, reaches the parabrachial nucleus, generating emotional, affective, and physiological manifestations of fear and anxiety [58]. The vestibular system is also anatomically connected to the locus coeruleus, raphe nucleus, and hypothalamus, providing even greater interplay between balance, sensorimotor integration, and emotional manifestations. Monoaminergic modulation of this system affects balance control depending on emotional state, as in SD [23]. In turn, changes in the sensory system or in the integrative system (cerebellum) may lead to distorted perception of the surrounding world, inability to predict events, dysfunction in decision-making related to maintaining balance, which can provoke chronic stress and anxiety [59].

As already noted, the LDST enables the assessment of the same parameters as the classical Suok test, yet scoring multiple additional endpoints [3,23] (Table 1) and is conceptually similar to the light–dark box anxiety assay (traditionally used to assess rodent anxiety [25,26]), and some other light-dark behavioral tests [60,61]. Supporting its validity, highly anxious BALB/c mice display a clear preference for the dark sector in both the light-dark choice test [62] and the LDST [3]. Thus, employing this modified version of the Suok test can help detect both anxiety-like states and resilience to anxiety, also enabling the investigation of the effects of various stressors and/or pharmacological substances [3,16,63].

Table 1
Selected examples of evaluation of various CNS deficits using the Suok test in rodents.

Disorders	Behavioral deficits in the Suok test (species)	References
Neurodegenerative disorders		
Parkinson's disease Multiple sclerosis	Motor dysfunctions, such as gait and coordination disorders (rats)	[11,82,89,90] [130]
	Motor sensory and vestibular dysfunctions (rats)	
Motor incoordination		
SD/SSD* and callosal deficits	High anxiety level and poorer motor coordination (mice)	[3]
Trauma		
Traumatic brain injury (TBI)	Motor dysfunctions (slipping of the hind legs, mice)	[91] [14]
Burn skin injury	Anxiety-like behavior and sensorimotor disintegration (rats)	
Prenatal CNS deficits		
Fetal alcohol spectrum disorders (FASD)	Motor, sensory and vestibular dysfunctions (mice)	[7,55]
Prenatal nicotine exposure	Deficits in sensorimotor integration and decreased directed exploration (mice)	[8]
Maternal hypomagnesemia	Anxiety-like behavior, with reduced head dips (mice)	[6]
Prenatal stress exposure	Motor, sensory and vestibular dysfunctions, such as increase in slips and falls (rats)	[131,132]
Paternal alcohol consumption	Sensorimotor disintegration (mice)	[7]
Other		
Gulf War Illness (GWI)	Anxiety-like behavior and sensorimotor disintegration (mice)	[13,57]
Autism spectrum disorder (ASD)	Decreased locomotion and exploratory behavior (mice)	[76]
Aging	Decreased locomotion and exploratory behavior (mice)	[87]

* Sensorimotor- and stress-evoked sensorimotor disintegration

In addition to novelty-evoked anxiety/neophobia per se, the Suok test triggers the fear of height, which both compete with the drive for exploratory activity. The beam or pole also represent a challenged environment for locomotion, and any disruptions in animal motor coordination and balancing become highly noticeable during the test [23]. In summary, albeit structurally similar to the stationary beam test (used to evaluate motor coordination and balancing [64,65]), the Suok test combines the principles of several traditional behavioral models, including the raised beam maze, open field, Swiss cheese board, and light-dark tests, allowing for the simultaneous induction and evaluation of anxiety and motor activity in animals [3]. Importantly, conventional rodent anxiety tests (e.g., the elevated plus maze, the light–dark test, the open field test, holeboard, mirrored chamber, and free exploratory paradigm) all assess anxiety-like behavior and neophobia evoked by novelty in a 2D (horizontal plane) space [66,67]. However, these paradigms are not suitable for investigating the vestibular system and sensorimotor integration/SD. In contrast, the Suok test enables the analysis of numerous parameters (Table 1) related to motor coordination, as rodents demonstrate a rich spectrum of spontaneous exploratory behavior in this test (in addition to motor/balance parameters), which is sensitive to various stress manipulations (Figs. 2 and 3 for summary).

The test is also sensitive to *strain differences* in rodent behavior [3,10], detecting contrasting phenotypes in anxious neophobic BALB/c mice vs. non-anxious C57BL/6 mice. The more anxious strain exhibits lower activity and higher anxiety in the Suok test - the distance travelled and the number of episodes of directed exploration were lower, while the delay in exiting the center, the number of stops, and defecations were higher compared to the non-anxious mice. Similar parameters were demonstrated in a group of mice subjected to acute stress (exposure to a rat) [3]. To confirm the effectiveness of the Suok test as a method of analysing motor coordination indices, 129S1/SvImJ mice, characterized by impaired motor coordination [68] and the absence of the corpus callosum, were compared to 'control' C57BL/6 mice. The 129S1/SvImJ mouse neuroanatomical deficit can impair the integration of motor and sensory information required for coordinated movement [69]. Similarly to the beam test, which shares structural similarities with the Suok test, 129S1/SvImJ mice showed more slips from the experimental setup and more pronounced anxiety than C57BL/6 mice [3]. Behavioral differences in this assay are also shown between the wild-type C57BL/6 mice and cannabinoid CB1 receptor knockout (*CB1-/-*) mice, focusing particularly on aspects of learning, memory, and anxiety-like behaviors [70]. The Suok test was notably effective in identifying these strain differences, as *CB1-/-* mice spend more time in the center of the apparatus, travel shorter distances, and exhibit increased immobility compared to the wild-type *CB1+/+* mice [70]. This behavior suggests a heightened anxiety-like response in *CB1-/-* mice, indicating that the absence of CB1 receptors may influence anxiety-related behaviors. Finally, the Suok test is capable of detecting SD, since following exposure to a rat (a muricidal predator), mice from different strains, in addition to anxiety, also demonstrate a marked deficit in motor coordination (SSD) [3,10].

4. Neuropharmacological applications of the Suok test

Mounting evidence shows that the Suok test behaviors can be dose-dependently altered by anxiogenic (e.g., pentylenetetrazole) and anxiolytic (e.g., diazepam and ethanol) drugs [16,71]. Reduced anxiety in

this test is predictably accompanied by lower exploratory behavior, whereas animals with higher anxiety cover a shorter distance, stay in the placement area longer, and exhibit impaired balance control [16]. Similar results were observed in experiments on rats demonstrating reduced exploration and poorer rod retention following an acute exposure to pentylenetetrazole [4]. Collectively, this suggested that the Suok test can be used as a reliable method to identify drug effects on both anxiety and SD. By simultaneously evaluating multiple domains at once (i.e., anxiety, motor coordination, balancing, SD), the use of the test reduces the need for a large number of animals [23]. Likewise, the test is easy to perform, does not require prior training of animals and in most cases demonstrates reliable responses already in the first trial [3,4].

Potentially anxiogenic pharmacological manipulations include prenatal exposure to nicotine or ethanol, as well as paternal ethanol consumption prior to conception [72–74], and the Suok test is sensitive to all these states evoked in rodents [7,8,74]. Maternal hypomagnesemia can also program anxiety-like behavior in offspring, which can be investigated behaviorally in this test [6]. Assessing two specific parameters of SD - the incidence of missteps and falls, a significant main effect of treatment was observed for missteps, indicating that the paternal ethanol exposure (PatEE) influenced SD, since female PatEE mice exhibit more missteps compared to female controls [75]. The Suok test was also employed to assess anxiety-like behaviors, with measures including the frequency of rearing and grooming, directed exploration, and latency to leave the centre of the bar, albeit without significant main effects of sex or treatment for these anxiety-related measures.

Furthermore, the Suok test can be applied for the comprehensive evaluation of behavioral status of model animals, e.g., focusing on mice with an autism-relevant phenotype induced by polybrominated diphenyl ether (DE-71) by showing decreased horizontal locomotion and exploratory activity, and increased unprotected stretch attend postures compared to the control group [76]. The test enables comparative behavioral analyses of the F0 generation (mothers) and the F1 generation (offspring) exposed to different levels of DE-71, probing transgenerational effects of polybrominated diphenyl ether exposure on anxiety and motor coordination.

As already noted, the Suok test can be used as an effective tool for evaluating the effects of various pharmacological substances [77]. Indeed, the assay has been successfully employed in studying the impact on rodent behavior of drugs, such as gamma aminobutyric acid (GABA) mimetics phenibut and baclofen [78], an anxiogenic GABA-lytic agent pentylenetetrazole, positive GABA-A receptor modulators anxiolytics ethanol and diazepam [16], as well as a wide range of other neuroactive substances, such as caffeine [79], cycloheximide [80], cytoflavin [81], quercetin [82], selank [83], semax [84], choline [55], cerebrolysin [85], and alpha-tocopherol during prenatal exposure [86], drugs that enhance brain metabolism [87], as well as heavy metal salts [15] and various plant-derived substances [5,17–21] (Table 2). For instance, rats chronically co-treated with caffeine and ethanol demonstrate higher behavioral activity in the Suok test than animals receiving ethanol alone, with females (but not males) also exhibiting more anxiety-like behavior [79]. Other Suok test studies report that cycloheximide (a naturally occurring fungicide) reduces, and cytoflavin (a complex drug for the treatment of diseases of the nervous system) increases, mouse locomotor activity and exploratory behavior [80,81]. Likewise, bioflavonoid quercetin exacerbates postural instability and gait disturbances in a rat model of proteasomal dysfunction in the nigrostriatal system, which can be utilized to model Parkinson's disease and characterize its progression using the Suok test [82]. The effects of pharmacological agents after stress exposure [21,83,84], in aging [87] and in models of various other diseases [15], are commonly assessed using the Suok test (Table 2).

5. Other applications of the Suok test

Potential deficits in vestibular function and motor coordination in rodents can also be evaluated using the Suok test, where key detectable

Table 2
Selected open questions related to using the Suok test in neurobehavioral research.

Questions
What are the effects of the major classes of neurotropic drugs on rodent phenotype in the Suok test?
How can pharmacological interventions that target specific neurotransmitter systems alter behaviors observed in the Suok test?
What additional factors should be considered when interpreting the Suok test results?
What changes to the Suok test apparatus can increase its sensitivity, accuracy and overall validity?
In what ways can machine learning algorithms improve predictive accuracy for anxiety-related behaviors based on data from the Suok test?
What additional data analysis tools can be applied to the results of the Suok test?
How can the Suok test be modified to assess anxiety in different species beyond mice and rats?
What changes can be introduced to the Suok test protocol the test to better capture anxiety in specific contexts, such as social anxiety or environmental stress?
How can the Suok test be used to better target anxiety in animals with different ages or developmental stages?
Is it possible to do vibration recording in the Suok test rather than video-recording?
Sensorimotor disintegration (SD) is common in schizophrenia [100]. How can the Suok test be used in behavioral modelling of schizophrenia?
How can the Suok test be employed to investigate the effects of hallucinogenic drugs on sensorimotor integration and anxiety-related behaviors, considering that these substances are known to induce sensorimotor disintegration and anxiety in both animal models and humans [103,104]?
Can the Suok test be effective for screening drugs with specific effects on the vestibular system (e.g., vestibular suppressants)?
How does the Suok test compare to other behavioral tests in assessing anxiety in rodent models? How do the assessed parameters of anxiety and sensorimotor integration correlate in the Suok test and in other similar behavioral tests such as open field, horizontal beam test, rotarod performance test and others?
How does social interaction during testing influence behavior in the Suok test?
How do behavioral responses measured in the Suok test correlate with physiological stress markers in rodents (e.g. corticosterone levels)?
How can the Suok test be integrated into a broader behavioral battery to enhance the assessment of anxiety-related behaviors?
What differences can be observed in the Suok test outcomes between male and female rodents?
How do hormonal fluctuations, such as those associated with the estrous cycle, impact performance in the Suok test?
How can variations in rodent housing conditions influence the results of the Suok test?
How does the length of time spent in the Suok testing apparatus affect the behavior of rodents observed during the experiment?
What are the potential effects of circadian rhythms on the performance of rodents in the Suok test? How do circadian disruptions affect anxiety behaviors measured by the Suok test in rodents?
How does maternal behavior affect offspring performance on the Suok test in later life?
In what ways could the combination of the Suok test and neuroimaging techniques improve our understanding of the relationship between the brain and behavior?
How do changes in diet or nutrition affect the behavior of rodents during testing using the Suok test?
How can the social hierarchy among rodents influence their performance during the Suok test?
How does chronic pain modulate anxiety-like behaviors as assessed by the Suok test?
How can behavioral data from the Suok test be integrated with genomic data to identify potential genetic markers for anxiety?
How can the presence of a new object or stimulus affect the behavior of rodents during the Suok test?
What is the potential translational value of the atypical (e.g., OCD-like or impulsivity-related) 'active jumping' off the rod/alley behavior in this test?

parameters include the number of falls, missteps, slipping of hind limbs, and movement speed (Figs. 2–3). The Suok test demonstrated a tendency to increased horizontal activity in S1BC (hybrid of 129S1/SvImJ and BALB/c) mice compared to S1 (129S1/SvImJ), S1N (hybrid of 129S1/SvImJ and NMRI) and S1B6 (hybrid of 129S1/SvImJ and C57BL/6) strains, whereas the latency to leave the center and the number of falls did not differ depending on the genotype [88]. Motor disturbances typical for certain rodent strains used to model human CNS disorders (e.g., Parkinson's disease) can be assessed in the Suok test by scoring the number of slips, distance travelled and movement speeds [11,82,89,90]. Another study examined the function of HSP70 (Heat Shock Protein 70) in the degeneration of dopaminergic neurons in a rat model of Parkinson's disease induced by lactacystin, where the Suok test following the knockdown of HSP70 gene reveals motor and coordination deficits in rats, underscoring the vital role of HSP70 in maintaining motor function in the context of neurodegeneration [90]. Likewise, congenital deficits in the interhemispheric connections, such as agenesis and dysplasia of the corpus callosum, affect the locomotor activity of rodents, also assessable using the Suok test. For example, 129S1/SvImJ rats, characterized by agenesis and dysplasia of the corpus callosum, presented more hindleg slips compared to mice with normal callosal structure (C57BL/6 strain), which, however, did not affect their test retention [3].

The application of the Suok test for studying locomotion and motor coordination in rodent models of brain injury is also highly relevant (Table 1). Targeted damage to the sensorimotor neocortex, induced by severing intracortical connections, results in injured animals displaying reduced horizontal locomotor activity and an increased number of paw slips over a 4-week period [91]. These findings confirm the notion of SD in animals with sensorimotor neocortex lesions. Thus, in addition to its utility for studying the consequences of brain injury, the Suok test can possibly be employed to map cortical regions that are critical for coordinating movement. This behavioral paradigm has the potential to facilitate the identification of specific areas within the sensorimotor neocortex that, when damaged, lead to SD and motor incoordination.

Moreover, the Suok test enables studying rodent habituation, evaluating their spatial working memory. For example, stressed mice show poorer habituation of their travelled distance, head dips, and the number of stops compared to the controls, demonstrating a consistent performance in the test, while in control mice, the traveled distance and the number of head dips per minute usually decreases over time [10]. These results underscore the importance of further research focusing on habituation changes and information processing in rodents under the influence of stress and memory-affecting substances [92].

Simultaneously recording multiple behavioral parameters, the Suok test can be used for a comprehensive evaluation of various CNS conditions. For example, probing the effects of prenatal stress on rats, the Suok test revealed higher vertical activity, the number of head dips over the edge of the platform, and orientations in immature males, while only vertical activity was elevated in adult males. These findings indicate significant age-related differences in behavioral dynamics. As the animals matured, the measures reflecting exploratory and anxiety-related behaviors predominantly returned to control group levels, which implies adaptations in adult animals [93]. Examining alcohol preference [94] and psycho-emotional status in burn skin injury [14] in rats, the test can be used for the combined assessment of motor and exploratory activity levels, as well as anxiety. Evaluation of anxiety-like behaviors reveals overt differences depending on alcohol preference, as the initial anxiety level observed before alcoholization in a group of male rats prone to alcohol consumption was lower than in males with less propensity. Moreover, rats that become more preferential towards ethanol by the end of the experiment have higher anxiety in the middle of the experiment, whereas this parameter declined in rats from the opposite group [94]. Animals with burn injury show signs of anxiety, such as lower horizontal activity (decreased rate of movement and fewer segments travelled), suppression of exploratory activity (less directed head movements and looking down), more defecation, and shorter self-grooming [14].

Other modifications of the Suok test involve placing a rat at one end of the beam with the animal home cage positioned at the opposite end [90]. Thus, in addition to the exploratory motivation, the rat has another incentive to move along the beam, which can be relevant when studying hypoactive animals. Furthermore, to assess the severity of motor impairments, in addition to evaluating the number of hind-limb missteps, the modified Mittoux scale [95] (e.g., ranging from 0 to 8) can be used, where 0 indicates normal motor function and 8 reflects severe, near-death impairments. This scale has been used to quantify the neuroprotective effects of adenovirus-mediated CNTF (ciliary neurotrophic factor) gene transfer [95]. The capacity to monitor alterations in motor function over time is crucial for assessing the efficacy of the neuroprotective intervention, and therefore the use of Mittoux scale as a supplement to the Suok test may enhance the model sensitivity and improve screening.

6. Challenges, limitations, and potential future applications

Like with any other neurobehavioral model introduced, the Suok test clearly has multiple limitations. For example, its protocol requires specialized equipment, such as a long elevated horizontal rod and a light-dark setup, which can be problematic for laboratories with limited space. Rodents of different strains may demonstrate variations in anxiety, activity, SD and balance in the Suok test, as well as altered sensory functions (e.g., vision or vibrissal sensation) [3,70]. There are also some species differences, as mice display more motor and exploratory activity, while rats collect more information and assess risks. For instance, in the Suok test, rats more often than mice adopt stretch-attend postures, which can be easily measured and analyzed.

Characteristic rodent 'barbering' (fur-trimming) behavior [96] in mice and rats can also influence the outcomes in the Suok test. For example, barbering may result in variations in vibrissae (whiskers) among the animals within the same cohort, which can adversely affect their sensory perception, basic stress level and navigational abilities/strategies within their environment [97]. Vibrissae are critical for spatial awareness and provide essential tactile feedback, enabling rodents to effectively explore and interact with their surroundings [98]. In contrast, rodents with shortened or absent (trimmed or plucked) vibrissae may display altered postural stability and a reduced motivation to engage in exploratory behaviors due to compromised sensory input [97]. Thus, such variability in whisker status can introduce confounding variables into the experimental results obtained in the Suok test, complicating the interpretation of the effects of pharmacological treatments or experimental conditions under investigation. In contrast, in more 'posturally stable' environments, such as the open field test, this sensory impact of barbering may be lesser, due to lesser reliance on precise whisker-mediated spatial navigation.

Furthermore, anxiety and aggression levels can vary considerably between different rodent strains, which in turn can impact the effectiveness of the Suok test [3]. For example, more aggressive and anxious mouse strains (e.g., BALB/c) show very low levels of barbering [96], but display reduced exploration and increased stopping behavior, which could mask the true levels of anxiety experienced by the animals [10]. Conversely, less aggressive strains (e.g., C57BL/6 J) may display increased exploratory behavior but common barbering, hence complicating strain comparisons in the Suok test. The negative correlation between aggression in rodent strains and barbering behaviors [96] can again impact rodent performance in the Suok test. For example, dominant mice that display reduced barbering may demonstrate distinct performance on anxiety-related tasks than subordinate mice with greater barbering, indirectly rising stress and anxiety levels [99]. Such variability can result in erroneous interpretations, emphasizing the importance of strain-specific behaviors for obtaining accurate results and generalizing findings across different rodent models.

The Suok test also requires careful calibration and standardization to

ensure consistent results within different laboratories, which is a challenging task since any variations in the setup or testing conditions can affect the validity of the results. Furthermore, the test involves handling and placing mice on the rod, which can cause stress and potentially influence the results. However, this stress factor is common for all behavioral models and can be mitigated by proper handling techniques and ensuring the animals are comfortable during testing [23]. Current Suok test protocols recommend placing the animal back to the rod (in the same location) if it fell from or jumped off the apparatus. Based on our own systematic experience with the assay, this is usually a rather infrequent phenomenon during the trials. However, the impact of falls and handling while returning the animal back to the rod on test sensitivity is unclear, and in some cases (e.g., if becoming frequent due to neurological deficits, impulsivity or OCD-like perseverations) may confound behavioral analyses. Moreover, while the test has been shown to be effective in mice and rats, its generalizability to other species is not yet established, meriting further studies.

In addition to anxiety and motor deficits, the Suok test can potentially be utilized to investigate some other complex CNS disorders, such as schizophrenia, by assessing anxiety-related behaviors and SD commonly seen in individuals with the disorder [100]. Moreover, it can possibly assess the effects of antipsychotic and anxiolytic drugs on anxiety and motor behavior, helping identify behavioral changes that may correlate with therapeutic effects. Additionally, the test can likely be adapted to study the interplay between anxiety and schizophrenia, as these disorders frequently co-occur [101], providing insights into their complexity and improving our understanding of novel therapeutic strategies. Similarly, the sensitivity of the Suok test to sedative agents (e.g., of ethanol or diazepam) suggests its potential for measuring sedative and nonspecific drug effects, such as pharmacogenic ataxia [102]. Evaluating changes in anxiety-related behaviors and motor coordination, the Suok test can also discern the impact of these drugs on sensorimotor integration and overall activity levels, which is of great practical importance. Such identification of nonspecific effects is crucial for the development of safer and more efficacious pharmacological treatments, and can reveal potential side effects associated with sedative properties.

The Suok test can also become a valuable tool for screening drugs that specifically affect the vestibular system, particularly vestibular suppressants. For example, the test may help identify drugs that impair vestibular function or cause ataxia by measuring increases in hind leg slips and falls from the elevated beam, indicating disrupted sensorimotor integration. Additionally, since vestibular disorders are often linked to anxiety in both animals and humans, the test can detect these anxiety-related behaviors. By providing measures of horizontal and locomotor activity, the Suok test helps differentiate vestibular-specific effects from general motor impairments, allowing for standardized comparisons of various vestibular suppressants, such as antihistamines, anticholinergics, and benzodiazepines. This capability aids in elucidating the mechanisms by which these drugs impact vestibular function and associated behaviors. Furthermore, the simplicity and efficiency of the test make it suitable for high-throughput screening of potential vestibular agents, facilitating the rapid identification of compounds with desired effects on the vestibular system.

The test has the potential to be employed in the investigation of the effects on anxiety and SD induced by hallucinogenic drugs. For example, it can be used to examine how hallucinogens like lysergic acid diethylamide (LSD), 4-phosphoryloxy-N,N-dimethyltryptamine (psilocybin), or N, N-dimethyltryptamine (DMT) affect anxiety-related behaviors and SD in animal models, which is important because hallucinogens are known to modulate anxiety and mood states in humans [103]. Additionally, as hallucinogens often cause SD, the test is expected to be able to provide insights into how these drugs impact the integration of sensory and motor functions. Furthermore, the test can be employed to study potential lasting behavioral changes following hallucinogen exposure, which is relevant to understanding conditions like hallucinogen persisting perception disorder (HPPD) [104]. Albeit not yet tested directly, the test also can possibly enable standardized comparisons between different hallucinogenic substances in terms of their behavioral impact, and by assessing these behavioral changes, the test may provide insights into the addictive potential of various hallucinogenic substances. Ultimately, findings from rodent models using the Suok test can inform human clinical research on hallucinogens, contributing to a better understanding of the effects and potential therapeutic applications of these compounds.

Rodents, particularly mice and rats, emit ultrasonic vocalizations (USVs) for various purposes, including maternal communication, the conveyance of emotional states and social interactions [105,106]. These vocalizations can serve as signals of distress (e.g., isolation-induced calls from pups to attract maternal attention), or be emitted for the facilitation of mating behaviors and the establishment of social bonds. The incorporation of USV detection into the Suok test protocol, if implemented, can markedly enhance the assessment of anxiety in animal models, providing objective, quantifiable measures of vocalizations to minimize observer bias and subjectivity in the evaluation of stress and depression. This can enable capturing subtle vocalizations that indicate the animal's emotional state, thereby providing additional data on the effects of experimental conditions or pharmacological interventions. Furthermore, USV detection is a widely used non-invasive approach that permits continuous monitoring of the animal responses without introducing additional stressors associated with direct observation or handling [105,106]. However, while USV analysis can certainly augment behavioral phenotyping in the Suok test, its utility may also be somewhat limited. For instance, in anxiety-provoking paradigms (e.g., the elevated plus maze), rats may emit appetitive 50-kHz calls rather than aversive 22-kHz vocalizations, potentially reflecting exploratory motivation rather than distress [107,108]. Thus, the inclusion of USV recording in the Suok test may require careful interpretations in order to properly distinguish between various behavioral states such assays may contribute to. Likewise, the Suok test may also be valuable for behavioral phenotyping of genetically modified animals, assessing the impact of genetic manipulations on anxiety, motor function, and their interactions with high versatility.

Clearly, visual recording is not the only modality available for Suok testing. For example, the test may be enhanced by incorporating vibration recording and behavioral transcription, similar to [109], to provide a more nuanced understanding of animal behavior without relying solely on video recording. Integrating vibration sensors into the Suok test apparatus can capture fine movements and interactions of animals navigating the elevated beam, detecting vibrations that provide real-time data on activity levels and coordination. This data can be analyzed and transcribed into behavioral metrics, such as the number of slips, falls, and exploratory behaviors, using automated software algorithms to interpret vibration patterns. This method allows for efficient data analysis and the identification of subtle behavioral changes that might be overlooked in traditional video analyses. Additionally, using vibration recording and automated transcription minimizes human error and bias in data collection, resulting in more reliable and reproducible results. In a similar vein, remote thermo-imaging of rodents in this test may also be possible, similar to other behavioral assays [110], with an added value of better detecting the body temperature (due to a fuller body exposure to side-directed sensors in the Suok test vs. top-positioned open field thermo-sensors) and its real-time dynamics. The latter may not only assess rodent behavior in some environments without the need to rely on video detection, but can also be relevant to simultaneously characterizing some other important and sensitive rodent phenotypes, such as stress-induced hyperthermia [111,112], hence markedly enriching the spectrum of behavioral endpoints, phenotypes and phenomena tested.

Another interesting, creative and feasible, but yet still hypothetical, area of application of the Suok test can be using heated rod (instead of that of room temperature) to assess the interplay between locomotion, exploration and nociception. For example, rodents will likely actively

jump off the heated rod to avoid hyperthermia and pain. Similarly to the hot plate nociception assay [113,114], in which the rodent is placed on an enclosed hot plate and measured the latency to lick a hindpaw or jump out of the enclosure [115]. Thus, if implemented, this modified protocol may enable varying temperature of the horizontal rod in the Suok test apparatus in order to simultaneously assess in real time some neurobehavioral phenomena related to stress and pain (e.g., stress-induced analgesia [112,116]).

In addition to heating, applying electric currents to the metal rod of the Suok test may also be promising and result in a potential modified assay to assess rodent behavior more fully. For example, using a set or varying strength of electric current, this can serve as either an additional anxiogenic stress factor (to assess rodent anxiety) or as a pain stimulus (to assess nociception; see [117,118] for example). Likewise, using a strong electric current in the Suok test during the trial may be similar to the foot shock model of stress [119,120], empowered by possibility of assessing the entire spectrum of the Suok test behaviors once such shock is delivered. Further 'potentiated' modifications of the Suok test setup, such as using a smaller-diameter, slippery/oiled, inclined, shaking, swinging, vibrating or even rotating rod (i.e., somewhat resembling rotarod or accelerod assays), all may be suggested to evoke additional stress and/or postural instability in this assay. Although these modifications of the Suok test procedure remain to be tested experimentally, this line of research warrants further scrutiny.

Autism spectrum disorder (ASD) is closely linked to anxiety and sensorimotor impairments, with many individuals exhibiting sensory over-responsivity and motor coordination difficulties [121]. These sensorimotor challenges can exacerbate social communication deficits and contribute to heightened anxiety levels, creating a cycle that complicates the clinical presentation of ASD [122]. Rodent models exhibiting autism-like traits can be utilized to elucidate the contributions of anxiety and sensorimotor impairments to the overall phenotype of ASD models. Furthermore, the efficacy of pharmacological agents designed to alleviate symptoms, such as anxiety, can be evaluated in a model of ASD. The Suok test can be integrated with other behavioral assessments to create a more comprehensive view of the social deficits that are characteristic of ASD. Combining the results from the Suok test with those from social interaction tests, as well as USV analyses discussed above, may help gain a deeper understanding of the ways in which anxiety and sensorimotor impairments impact social behavior in rodent models of ASD. For example, placing two animals on the same Suok test apparatus and monitoring them together as a unit to assess anxiety, locomotor activity, SD, social interaction and aggression, may also be possible.

The Suok test is also likely useful to study impulsive behavior in rodents, as impulsivity can be inferred from the frequency and immediacy of the behavioral response when faced with anxiety-inducing stimuli or novel environments [123]. For instance, a rodent exhibiting high impulsivity may jump off the elevated surface without hesitation, indicating a lack of behavioral inhibition. Alternatively, this pattern may also be related to repetitive stereotypic behavior. Thus, regardless of its causes, such atypical behavior can be quantitatively measured in the Suok test by recording the number of jumps and the latency to jump after exposure to a stressor or a novel object. In addition to jumping behaviors, rodents in LDST typically display a natural aversion to brightly lit areas due to their instinctual fear responses [23]. However, an impulsive rodent may exhibit rapid transitions from the dark chamber to the light chamber, reflecting an inability to weigh the potential risks associated with exposure to light. This impulsive switching behavior can be assessed by measuring the latency and frequency of entries into the light chamber, as well as the time spent in each chamber. Furthermore, combining the Suok test with pharmacological interventions may help explore how various treatments impact impulsive behaviors and anxiety levels in various rodent models.

The cerebellum is critical for sensorimotor integration, facilitating the coordination of sensory inputs and motor outputs to produce smooth and precise movements [124]. This function is accomplished through the convergence of sensory information, motor learning, and predictive processing, which enables real-time adjustments based on feedback. The Suok test evaluates the ability of laboratory animals to integrate sensory information with motor responses [3]. Observed abnormalities during this assessment may suggest dysfunctions in the cerebellar circuits involved in sensorimotor integration. Consequently, this provides an opportunity to phenotype animal models exhibiting cerebellar pathologies and to screen pharmacological agents aimed at treating these disorders.

The use of artificial intelligence (AI) applications also has the potential to markedly enhance the analysis of the Suok test data, through the automation of processes and the improvement of the accuracy of behavioral assessments. Tools such as DeepLabCut and SimBA have the capacity to automate the classification of behaviors observed during the test, including exploration patterns and motor coordination metrics [125]. This enables real-time analysis and reduces the potential for human error in interpreting results. Similarly, the SuperAnimal tool can be employed to facilitate the efficient analysis of the Suok test data, thereby automating the behavioral assessment process [126]. For example, this tool can automatically track and classify a range of behaviors exhibited by rodents, including horizontal locomotion, vertical rearing, and stopping activity. Providing objective behavioral analysis, SuperAnimal can facilitate identifying anxiety levels and motor coordination impairments in response to different stressors or treatments. Furthermore, LabGym enhances these tools by integrating data from other experiments, thereby providing a comprehensive view of how genetic or pharmacological interventions affect anxiety phenotypes and motor coordination [127]. Additionally, AI tools facilitate data visualization, thus helping interpret complex results and highlight robust behavioral differences between experimental groups with greater ease. Collectively, these and other AI applications are expected to streamline the analysis process, improve accuracy, and facilitate deeper insights into the behavioral, neurological and physiological outcomes observed in the Suok test.

7. Concluding remarks

In summary, despite the widely acknowledged necessity for the development of novel approaches to access behavioral correlates of modification of brain function [128], progress in this area remains limited. One recent strategic approach involves the use of 'hybrid' behavioral tests, wherein one test (e.g., the forced swim test) can be integrated with another assay either as a battery (e.g., characterizing rodent swim-induced self-grooming under stress and non-stress conditions [129]) or as a single 'combined' assay (e.g., the light-dark forced swim assay [61]). This hybrid approach markedly reduces the duration of the experiment and the number of animals used in the study, while also greatly enhancing the 'synchronization' of the evaluated parameters (e.g., motor and sensory functions). Importantly, the Suok anxiety test itself, and especially its light-dark modification, can clearly be categorized as 'hybrid' tests, and be applied for the concurrent in-depth assessment of multiple (i.e., anxiety, locomotor and vestibular) functions, as well as complex phenomena, such as anxiety-evoked SSD.

Overall, the Suok test emerges as a useful tool in neurobehavioral research, particularly in the assessment of anxiety and vestibular disorders. The methodological strengths of the test, including its ability to differentiate between anxiolytic effects and SD, support its utility in pharmacological research as well. The ability to evaluate a wide range of behavioral parameters across multiple domains (Figs. 2–3), such as exploration, anxiety levels, and vestibulomotor functions, fosters a comprehensive understanding of the effects of various pharmacological agents on rodent behavior. Moreover, the test's procedural simplicity, adaptability to different experimental conditions and contexts, potential for high-throughput screening and amenability to conceptual and technical innovation (including the use of AI for data analyses, robotic

handling of animals and creative modifications of the apparatus discussed above) can facilitate preclinical CNS research in rodents.

The findings derived from the Suok test may not only contribute to the understanding of the neurobiological underpinnings of anxiety and motor coordination but also pave the way for the development of targeted pharmacological interventions. Future research can focus on further refining the Suok test methodology and exploring its applications in diverse contexts, including assessing the effects of novel compounds and age-related behavioral dynamics. Likewise, the potential use of this test for other (e.g., non-rodent) laboratory or veterinary animal species also remains to be tested, and may spearhead the renewed interest to this multi-domain behavioral assay. Continued validation and expanding the use of the Suok test can improve our understanding of various complex behavioral phenomena and help develop novel therapeutic strategies for anxiety and vestibular disorders, as well as SD. The demonstrated sensitivity of the Suok test to prenatal stress [131,132] is beneficial for in-depth behavioral characterization of delayed neurobiological effects in vivo. Finally, the robustness and practical ease of the test make it valuable for hands-on training of students in neurobehavioral methods [133].

Author contributions

All authors have extensively contributed to this manuscript. AVK conceived and coordinated the project. All authors have participated in data collection, analysis and interpretation. VDR, AM, DSG and MSA drafted the manuscript. VDR, AM, AVK and MSA participated in critical review and further revision of the manuscript. AVK provided overall supervision of this project. All authors contributed to critical discussions and finalizing the manuscript before submission and have approved its final form.

Declaration of Competing Interest

AVK is the original co-developer of the rodent Suok test [3,23]. He has no financial or other personal interests in this model, which is patent-free and has been made freely available to the global research community. Authors declare no other conflicts of interest.

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Data availability

Data will be made available on request.

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