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# Advances in understanding neural mechanisms of social dominance

Tingting Zhou[1,2,3], Carmen Sandi[4,5] and Hailan Hu[1,2,5]

Dominance hierarchy profoundly impacts social animals' survival, physical and mental health and reproductive success. As the measurements of dominance hierarchy in rodents become established, it is now possible to understand the neural mechanism mediating the intrinsic and extrinsic factors determining social hierarchy. This review summarizes the latest advances in assay development for measuring dominance hierarchy in laboratory mice. It also reviews our current understandings on how activity and plasticity of specific neural circuits shape the dominance trait and mediate the 'winner effect'.

**Addresses**
[1] Center for Neuroscience, Key Laboratory of Medical Neurobiology of the Ministry of Health of China, School of Medicine, Interdisciplinary Institute of Neuroscience and Technology, Qiushi Academy for Advanced Studies, Zhejiang University, Hangzhou 310058, PR China
[2] Mental Health Center, School of Medicine, Zhejiang University, Hangzhou 310013, PR China
[3] Institute of Neuroscience and State Key Laboratory of Neuroscience, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, University of Chinese Academy of Sciences, Shanghai 200031, PR China
[4] Brain Mind Institute, School of Life Sciences, Swiss Federal Institute of Technology Lausanne, EPFL, Lausanne, Switzerland

Corresponding authors: Sandi, Carmen (carmen.sandi@epfl.ch), Hu, Hailan (huhailan@zju.edu.cn)
[5] These authors contributed equally to this work.

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## Introduction

Social dominance is a universal phenomenon among social animals, ranging from insects [1], fish [2], to rodents [3] and primates [4]. Dominant individuals win more frequently in social competitions. Dominance status strongly impacts an animal's survival, physical and mental health and reproductive success [4–6]. A lack of motivation to compete in social contests may prevent individuals from realizing their potential. Therefore, understanding the central neural mechanism determining social hierarchy status is of critical importance.

Both intrinsic (physical and mental factors that are inherent and located within, for example, body size/strength, courage/fear, grit/persistency, stress level) and extrinsic factors (factors that are not inherent, acting from the outside, for example, environment, state of ally and opponents, experience such as history of winning/losing) contribute to social status determination. To understand the neural mechanisms underlying these intrinsic and extrinsic factors, simple and robust measurements for social dominance hierarchy are essential. In this review, we summarize the latest advances in the development of social dominance assays. We will also discuss the neuroendocrine regulation and circuit-specific neural activity as two examples of intrinsic factors, and the history of winning/losing as an example of extrinsic factor, and review the major findings in understanding how those factors determine social dominance status.

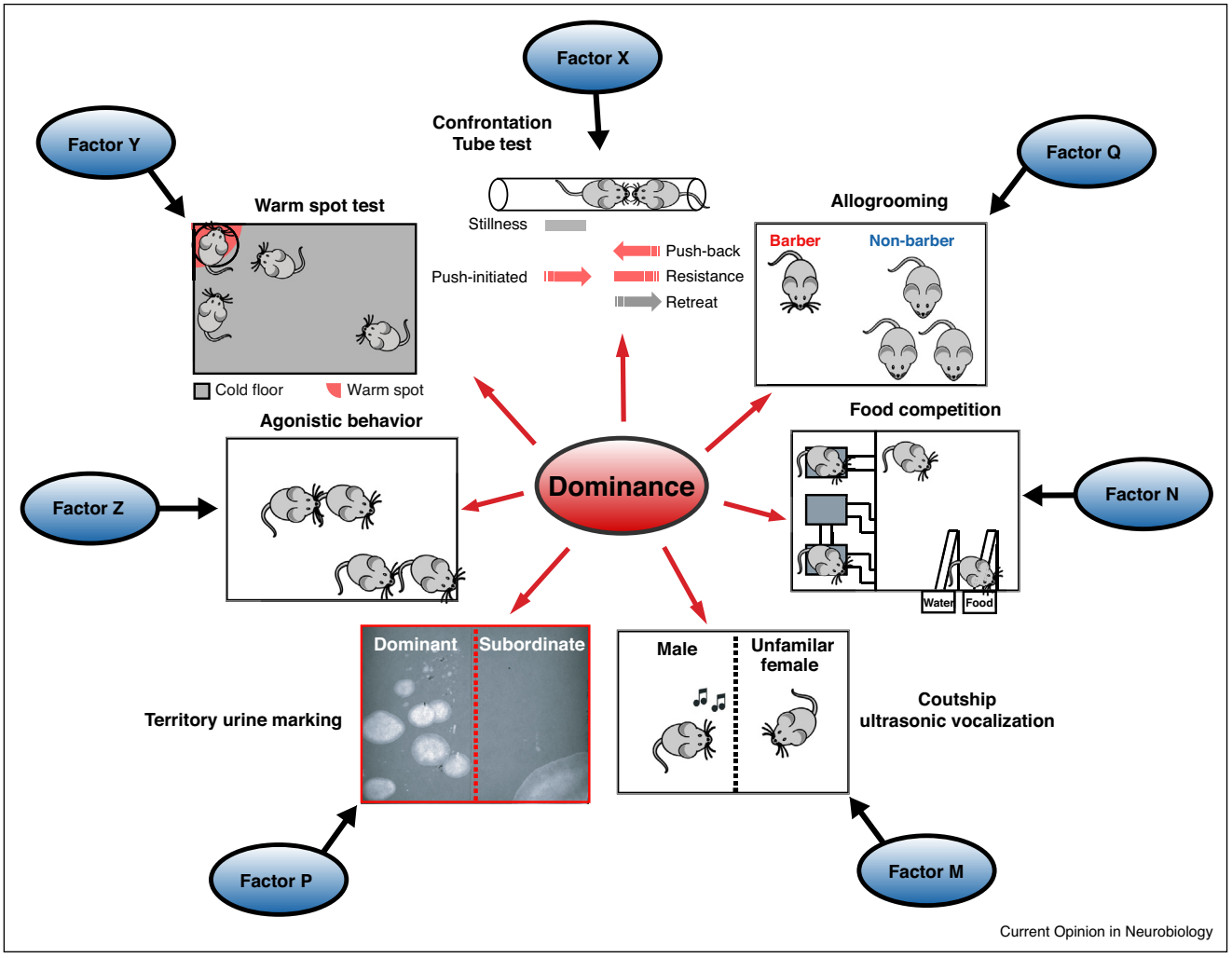
## Measurements of dominance hierarchy in laboratory mice

### Tube test

The tube test was developed in 1961 to measure dominance tendency between different mouse strains [7]. For a long time, it was used as a standard assay to screen the behavioral phenotypes of genetically modified mouse lines [8]. Wang *et al.* established in C57Bl/6 inbred cagemate mice that dominance ranks derived from the tube test are highly linear, stable, and correlate well with ranks derived from several other measures that reflect dominance hierarchy, including barbering, courtship ultrasonic vocalization, food competition in the visible burrow system, territory urine marking, and agonistic behaviors [9] (Figure 1). Tube test is simple and robust, introducing little stress and without causing injuries to the animals. It has since been used to investigate social dominance in mouse models of schizophrenia [10•], and the impact of dominance status on urination [11•], social interaction [12•], and vulnerability to social defeat [13••].

To analyze the detailed behavioral interactions during a tube test, Zhou *et al.* conducted a fine-grained video analysis [14••]. They quantified both behaviors generated voluntarily when mice faced an opponent in the tube (push-initiation) and the coping response when the opponent generated a push (push-back, resistance or retreat, Figures 1 and 2). These detailed analyses revealed insights on the potential internal states during social

**Figure 1**




Different measures of dominance in mice (modified from Wang *et al.* [9]). Performance in each of these paradigms is commonly regulated by dominance but also depends on sensory and motor factors unrelated to dominance (factors M, N, P, Q, X, Y or Z) — for instance, cold tolerance for the warm spot test or agility for the tube test. To rule out the interference of these other factors, we advise using more than one behavioral paradigm to measure social rank, especially between mice of different genetic backgrounds or with drug treatments.

competition: Do mice win by initiating more pushes or by being more persistent and resisting more pushes, or both? Do they lose because of lower endurance or by avoiding social engagement and initiating retreat voluntarily? Indeed, Zhou *et al.* found that winner mice initiated more pushes with longer duration, generated more push-backs and resistance when being pushed. In contrast, loser mice showed a higher probability of retreat (Figure 2). Understanding the whole process rather than only the outcome may help rule out undesirable secondary effects. For example, a less interesting scenario of winning might be caused by the mouse remaining still all the time until the opponent retreats. It is important to distinguish these possibilities especially when analyzing animals with genetic modifications or with drug treatments (Figure 1). Defects in locomotion, social memory and muscle strength also need to be ruled out before conclusions about social dominance can be made [14••].

## Warm spot test

In addition to the assays mentioned above, a novel social hierarchy paradigm — the warm spot test — has been recently developed, making use of animals' desire to stay warm [14••]. In this test, four cagemate mice are placed on an ice-cold floor with a warm spot in the corner, which can only accommodate one mouse at a time. Mice show competition to occupy the warm corner (Figure 1). The amount of time each mouse occupies the warm spot within the 20-min test is used to score social dominance. The warm spot test mimics the natural competition where the resources are limited and dominant individuals pay more efforts to occupy the desirable territory. Social

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