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The tendency for social submission predicts superior cognitive performance in previously isolated male mice

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The imposition of subordination may negatively impact cognitive performance in common social settings (e.g., the classroom), and likewise, laboratory studies of animals indicate that the stress associated with social defeat can impair cognitive performance. It is less clear whether an animal's *predisposition* for social subordination (i.e., a tendency that is expressed *prior* to experience with social defeat) is related to its cognitive abilities (e.g., "general" intelligence). Using genetically diverse CD-1 male mice, here we determined that in the absence of adult experience with social hierarchies or social defeat, the predisposition for social subordination was associated with superior general cognitive ability (aggregate performance across a battery of five learning tasks). The tendency for social subordination was not dependent on the mice' body weight, but both general cognitive ability and the tendency for social subordination were directly related to high stress reactivity (i.e., free corticosterone elevations induced by mild stress). This pattern of results suggests that submissive behavior and sensitivity to stress may be associated with superior cognitive *potential*, and this can reflect a native predisposition that precedes exposure to social pressures. More broadly, these results raise the possibility that socially subordinate animals evolved compensatory strategies to facilitate their survival, and that absent the *imposition* of subordination, normally submissive individuals may be better prepared for cognitive/academic achievement.

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1. Introduction

Among humans, the imposition of subordination (e.g., in the classroom) may produce circumstances that are detrimental to learning, such as elevated stress levels or a failure to effectively engage one's environment (Baumeister et al., 2002). Like humans, in their native environments, mice live in social groups, and socialization can improve cognitive performance in laboratory mice relative to mice housed in social isolation (Chida et al., 2006; Voiker et al., 2005). However, it has also been observed that the imposition of social subordination (which is often imposed on subsets of animals in many social groups) can impair cognitive performance in mice (Colas-Zelin et al., 2012; Fitchett et al., 2005). These patterns of results indicate that the benefits of social interactions can vary according to an animal's position in a social hierarchy, a conclusion supported by the observation that stress reactivity (e.g., corticosterone elevations) can covary with an animal's social status (Sapolsky, 2005). Despite the ramifications of these observations, there have been few attempts to elucidate the relationship between an animal's *predisposition* to behave in a dominant or subordinate manner and its innate cognitive abilities (but see Mery and Kawecki, 2003; for an example in *Drosophila*, and Cole and Quinn, 2012; for an example in birds). This neglect is significant, given that recent theories in evolutionary biology have suggested that humans began to form social groups at a time when testosterone levels (which is associated with aggressive behaviors) among males dropped (Cashdan and Downes, 2012). Not surprisingly, with decreased testosterone levels and socialization came a pattern of advances indicative of rapid increases in intelligence (Dawson, 1972).

To fully understand the relationship between innate tendencies toward submissiveness and intelligence, it would be necessary to isolate individuals from prior experience with social hierarchies (and the aggressive behaviors that are embedded in them) and then assess their cognitive abilities. In this regard, the use of mammalian animal models such as the mouse can be especially useful because individuals can be safely housed individually after the time of weaning (and long prior to adolescence). In the past, we have developed behavioral and analysis methods with which it is possible to characterize the general cognitive ability of outbred laboratory mice (Kolata et al., 2005; Matzel et al., 2003; Matzel et al., 2006; Wass et al., 2012), and this cognitive trait has been described as qualitatively analogous to what is described in humans as intelligence (Blinkhorn, 2003). This approach makes it possible to ascertain the degree to which social submission and general cognitive ability are related. Furthermore, we can then assess whether either of these innate traits are associated with other possible influences such as physical stature (e.g., body weight) or stress reactivity. While this issue has been partially addressed with both an experimental approach (i.e., selective breeding of *Drosophila* for their ability to form a simple associations, followed by an assessment of their competitive fitness; Mery and Kawecki, 2003) as well as a correlational approach (a comparison of problem solving ability to competition for food among wild great tits; Cole and Quinn, 2012), the present approach extends these prior results in three principal ways. First, we explored the relationship between general cognitive performance and tendencies for social submission in a mammalian species (genetically heterogeneous mice). Second, rather than a single learning task, in this study we assessed the performance of mice on a battery of five diverse learning tasks, and thus can draw conclusions about the animals' more general cognitive ability (c.f., "intelligence"). Lastly, in the present case, all mice were socially isolated since prior to adolescence, and were thus naïve to experience with aggression-based social hierarchies. Consequently, any relationship between submissive tendencies and general cognitive ability is not likely to reflect prior experience with defeat stress or aggressive social interactions.

Here, we used 64 outbred, non-littermate CD-1 mice that were individually-housed before sexual maturity (the time at which dominance hierarchies begin to emerge in mice). The mice were approximately 70 days of age (young adults) at the start of testing. CD-1 mice were chosen because they express genetic variability comparable to wild mice, and non-littermates' social interactions are less likely to be influenced by innate or acquired familial interactions. We first assessed these mice on a battery of five cognitive tasks designed to evaluate abilities in different learning domains, and the general cognitive ability of each animal was characterized according to its aggregate performance across all tests. Following the completion of the learning battery, we categorized the mice within a dominance hierarchy based on a test of aggressive social interactions. We assessed a subset of these animals (n = 32) on an additional test of social dominance (urine marking, which does not require interactions between animals) prior to the social aggression test. In addition, we measured in this same subset of animals the levels of corticosterone elevation in response to mild environmental stress (isolation on an elevated platform, which induces an intermediate level of corticosterone elevation). In this manner, it was possible to determine the relationship of general cognitive abilities to social dominance in adult animals not previously exposed to a social hierarchy. In addition, we tested the relationships between cognitive abilities and the tendency for social submission to the animals' physical "stature" (measured by body weight) and/or their hormonal responses to environmental stressors.

2. Methods

2.1. Subjects

Sixty-four outbred, male, non-littermate CD-1 mice were obtained from Harlen Sprague-Dawley, and arrived in our laboratory at approximately 35 days of age. This strain exhibits wide behavioral and genetic variability (similar to wild populations), and thus are well-suited for the study of individual differences. We used non-siblings to avoid familial and genetic similarities that might influence social interactions.

Upon arrival (and before sexual maturity, which occurs between 50 and 60 days of age), the mice were individually-housed in clear shoe-box cages and were maintained on ad libitum food and water (unless otherwise noted) in a temperature-controlled vivarium on a 12-h light/dark cycle. The mice were adapted to these conditions for 4–5 weeks prior to the start of experimentation. During this period, each mouse was handled daily (removed from its cage and held by an experimenter for 60 s/day). All mice were approximately 70 days of age at the start of behavioral testing (at which time body weights ranged from 26 to 32 g), and testing was complete by 130 days of age.