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The mother as hunter: Significant reduction in foraging costs through enhancements of predation in maternal rats

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ABSTRACT

In previous laboratory investigations, we have identified enhanced cognition and reduced stress in parous rats, which are likely adaptations in mothers needing to efficiently exploit resources to maintain, protect and provision their immature offspring. Here, in a series of seven behavioral tests on rats, we examined a natural interface between cognition and resource gathering: predation. Experiment 1 compared predatory behavior (toward crickets) in age-matched nulliparous mothers (NULLs) and postpartum lactating mothers (LACTs), revealing a highly significant enhancement of predation in LACT females (mean = ~65 s in LACTs, vs. ~270 s in NULLs). Experiment 2 examined the possibility that LACTs, given their increased metabolic rate, were hungrier, and thus more motivated to hunt; doubling the length of time of food deprivation in NULLs did not decrease their predatory latencies. Experiments 3–5, which examined sensory regulation of the effect, indicated that olfaction (anosmia), audition (blockade with white noise), and somatosensation (trimming the vibrissae) appear to play little role in the behavioral enhancement observed in the LACTs; Experiment 6 examined the possibility that visual augmentations may facilitate the improvements in predation; testing LACTs in a 0-lux environment eliminated the behavioral advantage (*increasing* their latencies from ~65 s to ~212 s), which suggests that temporary augmentation to the visual system may be important, and with hormone-neural alterations therein a likely candidate for further study. In contrast, testing NULLS in the 0-lux environment had the opposite effect, *reducing* their latency to catch the cricket (from ~270 s to ~200 s). Finally, Experiment 7 examined the development of predatory behavior in Early-pregnant (PREG), Mid-PREG, and Late-PREG females. Here, we observed a significant enhancement of predation in Mid-PREG and Late-PREG females – at a time when maternity-associated bodily changes would be expected to diminish predation ability – relative to NULLs. Therefore, as with the increasing reports of enhancements to the maternal brain, it is apparent that meaningful behavioral adaptations occur that likewise promote the survival of the mother and her infants at a crucial stage of their lives.

Introduction

Life must adapt, a dictum both clear and unforgiving. Arguably, no other developmental milestone is exemplified by, nor more reliant on, the sudden and dramatic behavioral alterations observed in the maternal mammal (Kinsley and Lambert, 2006, 2008). As pregnancy progresses, the female is literally transformed from an organism that actively avoided offspring-related signals, to one highly motivated by those same cues to build nests, retrieve, group, groom, crouch-over, and care for young (Numan and Insel, 2003). Ancillary responses such as reference memory, spatial learning, foraging, and boldness improve in mothers compared to NULLs (Kinsley et al., 1999; Pawluski et al., 2006a,b). Such modifications arise early and are persistent, with neural benefits that last well into senescence (Gatewood et al., 2005). Evolutionarily, such enhancements likely reduce the maternal burdens associated with sheltering and feeding the vulnerable young, collectively strengthening reproductive fitness. That is, we presume that plasticity expressed in response to reproduction may translate into benefits to mother and, hence, offspring. Of the many behaviors that change as a function of pending or present maternity, therefore, what of predation, a major pillar of the rat's behavioral repertoire? We present here an example of a likely temporary but striking enhancement of predation as a result of reproductive experience.

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Whereas a large portion of the rat's diet consists of plant materials and detritus, rats are nonetheless omnivores and proficient hunters. They will prey on a variety of other animals, which they stalk, chase, attack, and eventually consume. Rats are opportunistic and adaptable in their food choices, having been observed preying on a wide variety of small animals, including invertebrates (Strecker et al., 1962); other rodents (Hsuchou et al., 2002); bats (Villa, 1982); birds (Atkinson, 1985); and amphibians and reptiles (Whitaker, 1978). Furthermore, predation toward insects is a behavior that rats easily display (Kemble et al., 1985). As these authors report, the insect prey (here, cockroaches) was more likely to be attacked in their tests, and was attacked more rapidly, than either other prey objects (mice), or conspecific aggressive targets (rats) regardless of the previous amount of social experience of the subjects; the data suggest, perhaps, an affinity for such small prey objects and efficient sources of food. In general, then, rat predation on insects is both natural and easily observed, highlights an evolutionary relationship extending deep into their biological pasts, and represents a likely bridge between laboratory examinations of behavior and the rat's natural proclivities. Hence, predatory behavior stands as a representative and natural test of the preparedness of rat behavior. The study of predator–prey relationships is interesting from a number of levels, from subtle to more obvious, and the behavior would likely benefit from both cognitive and motor modifications of the sort associated with the maternal brain.

For example, many recent data show that temporal adaptation is a hallmark of the maternal female. There are numerous reports of reproductive experience enhancing various aspects of the mother's behavior, including cognition (Bodensteiner et al., 2006; Buckwalter et al., 1999; Gatewood et al., 2005; Gonzalez-Marsical and Kinsley, 2009; Kim et al., 2010; Lambert et al., 2005; Pawluski et al., 2006a,b). Because predation in the maternal animal lies at the intersection of personal and offspring resource acquisition (viz., lactation), it serves as a valuable model for examining reproduction-induced modification of maternal behavioral repertoires. In the current set of seven behavioral experiments, we examined predation (which for the rat, we believe, is also an ethologically-relevant junction between cognition and resource gathering) in age-matched NULL, PREG and LACT rats. Later-PREG and LACT females are significantly better hunters than NULLs; their ability to track–attack-and-capture prey – an enhancement related to possible compensatory boosts in vision and motor skills – occurs at a time when the female is actually most unwieldy and reliant on collective incremental improvements to balance the costs of reproduction, both physically (a larger body size) and logistically (the substantial demands of young). This simple yet robust behavior may shed a light on the necessary behavioral expansions required of the mother at a time in her life when even the most incremental improvement may spell the difference between the mother's and her offspring's survival or not.

Materials and methods

Animals and reproductive experience

Approximately 138 adult (90–120 days) nulliparous (NULL) female Sprague–Dawley rats (Crl:CD[SD]BR), offspring of stock originally purchased from Charles River Laboratories, Inc. (Wilmington, MA) were used in the present set of experiments. These females either remained un-mated (NULL) or were timed mated in our laboratory. For the mated females, the day that a vaginal plug, or sperm in the vaginal lavage, was observed was designated Day 0 of pregnancy. The mated females were then removed from the male's cage and, together with the separate groups of un-mated NULL females, were housed individually in modified standard rat cages (20 × 45 × 25 cm polypropylene cages), the floors of which were covered with pine shavings. Food (Purina rat chow) and water were available ad libitum and all animals were housed in a reversed light:dark cycle (off from 0800–1800 h) and temperature (21–24 °C)-controlled testing rooms for the duration of the present work. All animals used in this study were maintained in accordance with the guidelines of the Institutional Animal Care and Use Committee (IACUC) of the University of Richmond (protocols #: 09-04-1 and 12-04-1) and in accordance with the *Guidelines for the Care and Use of Mammals in Neuroscience and Behavioral Research* [(National Research Council, 2003); University of Richmond's assurance number: A3615-01].

General predatory behavior procedure

All of the subjects were exposed to three-days of three 10-minute pre-exposures/habituations to the testing arena, a large (152.4 cm × 152.4 cm × 91.44 cm) open-walled enclosure. On Day 4, the animals were food deprived for at least 10 h. Testing consisted of a 5-min acclimation period in the open-walled arena, followed by placing the prey (an adult cricket, *Acheta domesticus*) opposite to the animal in the arena. We observed and recorded (with video documentation) the latency (out of 5-min/300-s) to capture the cricket and to begin to consume it (all but the last experiment, which took place in the dark; see experimental details below.) The data were collapsed to produce mean latencies (three-trials over three-days). We operationally-defined the predatory attack as the female attacking (an intentional movement toward the prey) and subduing the cricket, typically with the forepaws, preparatory to its being consumed. A small (<8%) subset of animals (slightly more in the NULL group, but not demonstrating a major trend for any group) caught the prey, but allowed the cricket to slip away at least once before consuming it. In these cases, we used the original latency to catch the cricket as the data point.

Specific experimental procedures

In Experiment 1, 90 days–120 days (nulliparous [NULL]) and Day five/six lactating mothers (LACT; n = 12/group) were food-restricted and habituated as described above, followed by the placement therein of the single adult cricket.

To control for potential differences in hunger motivation, Experiment 2 examined NULLs (n = 10) food-deprived for 20 h, twice as long as those in Experiment 1. These animals were compared with the NULL group from Experiment 1. In every other respect, these animals were treated identically to those NULLs in Experiment 1.

For Experiments 3–5, which examined potential sensory system enhancements in the maternal female, only LACT females were used. Experiment 3 examined possible modifications to the sense of olfaction via comparisons between controls and anosmic LACTs. LACTs in the anosmic group (n = 9) were lightly restrained and had their nares infused with an intranasal treatment of isotonic zinc sulfate ($ZnSO_4$; 10% in 0.9% saline). Control mothers (n = 9) were infused with 0.9% saline alone. Care was taken to ensure that the anosmic females cared for their pups, and that all pups displayed prominent milk bands during the conduct of the testing, indicating the LACTs' normal lactation and attention. Such anosmic effects typically last seven days (McBride et al., 2003), well within the window of our testing regimen. Post-testing, all animals were exposed to a hidden piece of cookie in their cages to determine the persistence of the anosmia. Any animal that investigated or found the cookie had its data removed from the group results.

In Experiment 4 we studied possible reliance on audition. Here, we tested LACTs (n = 7) in the presence or absence of white noise. We employed a gray plastic-housed white noise generator producing 65 dB of white noise, which effectively masked the sound of the cricket as it moved about the bedding (dimensions: 14 cm diameter; 12 cm height). LACT controls (n = 7) were tested as per the regular regimen, but with the white noise generator present but switched-off.

In Experiment 5 we examined general somatosensory sensitivity. LACTs (n = 9) were lightly restrained and had their vibrissae trimmed to within 1 mm of the facial fur. LACT controls (n = 9) were likewise