Activation of latent programs for maternal behavior

Eduarda Streit Morsch Elizabeth A. Amadei Roman Boehringer
Benjamin F. Grewe Pau Vilimelis Aceituno

Abstract

Maternal behaviors in mammals, which are critical for offspring survival, involve complex interactions between innate neural circuits and behavioral flexibility. This flexibility depends on environmental needs and external stimuli. Recent studies suggest that social transmission plays a crucial role in the acquisition of maternal behaviors in alloparental (non-maternal) subjects, particularly highlighting visual observation for virgin female mice to acquire pup retrieval behavior. However, the extent to which these behaviors rely on social transmission versus the activation of pre-existing, latent behaviors remains unclear. Here, we systematically investigated the necessity of social observation for maternal behavior acquisition, using a social transmission pup retrieval paradigm in pup-naive virgin female mice. Following the same protocol as previous studies, we compared retrieval performance on conditions that either allowed or prevented the visual observation of maternal demonstrations. Contrary to previous findings reporting substantial differences between these conditions, we found that virgin females readily acquired pup retrieval behavior regardless of their visual access to experienced mothers. We observed no significant correlation between maternal and virgin performance after task exposure. Detailed behavioral analysis revealed that the primary difference between mothers and virgins lay on the latency to initiate the behavior, but once started, virgins complete the retrieval as fast as mothers. Together, our findings show that pup exposure is enough to activate latent behaviors, and suggest that pup retrieval might not be transmitted by visual observation.

Introduction

Animals possess a variety of innate behaviors that allow for their survival, and they also possess the ability to acquire new behaviors through experience and exposure. An interesting behavior that falls in both categories is parental behavior, which animals express differently depending on gender and socio-sexual experience [1, 2]. For instance, in rodents, pup retrieval — the act of returning displaced pups to the nest — serves as a commonly used model for studying whether and how experience modulates innate behaviors. This behavior, consisting of locating pups astray from the nest, picking them up, and bringing them back, is particularly valuable as it is both stereotyped and measurable. Dams ("mothers") promptly rescue stray pups back to the

nest to avoid death by hypothermia, while pup- and sexually-naive females ("virgins") do not instinctively perform this behavior [3]. They can learn it depending on the animal's socio-sexual history and whether they have been exposed to dams and their litter [4, 5].

Recent work by Carcea et al. [6] proposed that observational learning plays a critical role in virgin mice acquiring pup retrieval behavior. Their study reported that virgin females learned to retrieve pups when the transparent barrier allowed them to observe maternal behavior, but most failed when the barrier was opaque. This finding suggested that visually observing an experienced conspecific is sufficient for behavioral acquisition, which implies a socially transmitted learning component. However, our laboratory did not reproduce the results. This discrepancy raises important questions about the fundamental mechanisms underlying virgin females acquiring maternal behaviors: Does the acquisition of these behaviors rely on social transmission, or does it reflect the emergence of pre-existing, latent behaviors that activate through exposure to pups alone?

In the present study, we systematically investigated the necessity of social observation for virgin female mice to acquire pup retrieval behavior. Using the same protocol that Carcea et al. [6] employed, we compared the performance of virgin females in transparent versus opaque barrier conditions across multiple sessions. Our findings challenge the notion that visual observation is necessary for acquiring pup retrieval behavior, suggesting instead that pup exposure alone may be sufficient to trigger latent maternal behaviors in virgin females. Our findings, in comparison to current literature, suggest that the pup retrieval task might be a flawed measure to test alloparental subjects acquiring maternal behavior through observation, and suggest that mice might use other cues than visual observation to perform the behavior.

Results

Naive females acquire pup retrieval behavior independently of visual observation

To investigate the role of social transmission in maternal behavior, we compared pup retrieval performance in pup-naive virgins under two experimental conditions: transparent or opaque barriers, which separated the demonstration from observation (Fig.1A). In line with the literature, mothers performed consistently well over all days (Extended Data Fig. 1A). Virgins showed substantial acquisition of retrieval behavior in both conditions: in the transparent barrier group, 12 out of 14 virgins (85.7%) successfully retrieved at least one pup in all sessions, while in the opaque barrier group, 10 out of 13 virgins (76.9%) demonstrated successful retrieval (Fig.1B). This revealed no significant differences in retrieval success ($p > 0.05$, Fisher's exact test). Similarly, the onset of virgin retrieval (i.e., the first session to retrieve at least 1 pup) did not differ based on barrier type (Fig.1C, log-rank test on cumulative Kaplan-Meier curve, $p = 0.310$). Note that four virgins retrieved on d0 (two virgins in each barrier group) 1B, which already contrasts the Carcea study [6], where no virgins retrieved.

To test whether barrier transparency and session day affected virgin mice performance, we conducted

a Linear Mixed Effects Model regression with barrier condition and sessions as fixed effects. Given that mothers and virgins paired with each other over days, we used the pair ID as a random intercept to account for the clustering of virgin mice with mother-virgin pairs (Table 1). We found a significant effect of training session ($p < 0.001$), with virgins showing significant improvement by day 3 ('d3', $\beta = 20\%$, 95% CI: 6.4-33.6%, $p = 0.004$, Fig. 1C) and day 4 ('d4', $\beta = 25.4\%$ 95% CI: 11.8 - 39%, $p < 0.001$, Fig. 1C) compared to baseline (prescreening, 'd0'). We found no significant effect of barrier type ($\beta = -0.11\%$, $p = 0.898$) or barrier $\times$ session interaction (all $p > 0.05$, Table 1), suggesting that only exposure, not barrier type, caused virgin performance to increase over days. The intraclass correlation coefficient (ICC ≈ 0.3) indicated moderate clustering within pairs, meaning that 30% of the variance in virgin performance results from animal pairing, supporting the use of mixed-effects modeling.

Term	**Coef.**	**SE**	**Z**	**p**	**95% CI**
Intercept	1.54	5.84	0.26	0.79	[-9.9, 13.0]
Barrier (Transparent)	-0.11	8.11	-0.01	0.99	[-16.0, 15.8]
d1	5.38	6.94	0.78	0.438	[-8.2, 19.0]
d2	9.23	6.94	1.33	0.183	[-4.4, 22.8]
d3	20.0	6.94	2.88	0.004	[6.4, 33.6]
d4	25.38	6.94	3.66	<0.001	[11.8, 39.0]
d1 × Transparent	2.47	9.63	0.26	0.797	[-16.4, 21.4]
d2 × Transparent	7.2	9.63	0.75	0.455	[-11.7, 26.1]
d3 × Transparent	12.14	9.63	1.26	0.207	[-6.7, 31.0]
d4 × Transparent	9.61	9.63	1.0	0.318	[-9.3, 28.5]
Log-likelihood			-594.62		
Group Var			131.248		
Residual Var			312.658		
ICC (Group Var/Residual Var)			0.296		

Table 1: **Mixed Linear Model Results:** Mixed-effects analysis revealed a significant main effect of session, but not barrier type or the interaction of barrier type $\times$ session. The intraclass correlation coefficient (ICC) indicates moderate clustering within pairs, thus validating the use of mixed-effects modelling. Coef: Coefficient. SE: Standard error. Z: Z-statistics. CI: Confidence interval. Group Var = Group variance, or random effect. Residual Var: Residual variance.

Given the moderately strong effect of animal pairing on explaining the variance in our data, we directly tested whether observing maternal behavior influenced virgin performance. We performed session-by-session Spearman rank correlations between maternal performance and virgin performance on the same session (Extended Data Fig. 1B). In both barrier conditions, correlations were weak and non-significant across all days ($p > 0.1$ for all sessions). These findings indicate that the quality of maternal demonstrations did not predict virgin performance.

To validate these findings and address potential concerns about our analytical approach, we confirmed our results using an alternative statistical framework. To ensure that the binomial nature of trial outcomes (successful retrieval = 1, failed retrieval = 0) did not affect our results, we used a Logistic Mixed Effects regression with a binomial Generalized Linear Model and logit link function. Again, the model revealed robust learning across all sessions while confirming the absence of barrier effects (Table 2).

Since these results contrast with previous reports, we decided to reproduce the standard two-way ANOVA

testing from Carcea et al [6]. The barrier type did not have a significant effect on virgin retrieval performance ($F(1, 25) = 2.68$, $p = 0.104$, Extended Data Table 4, Fig. 1C), whereas the session day significantly determined it ($F(4, 125) = 9.32$, $p < 0.001$, Table 1 and Fig. 1C). We found no significant interaction between barrier type × session on retrieval performance ($F(4, 125) = 0.35$, $p = 0.842$, Table 1 and Fig. 1C), indicating that barrier type did not affect the progression of retrieval performance over sessions.

Term	**Coef.**	**SE**	**Z**	**p**	**95% CI**
Intercept	-4.159	0.713	-5.836	<0.001	[-5.56, -2.76]
Barrier (Transparent)	-0.075	1.008	-0.075	0.940	[-2.05, 1.90]
d1	1.560	0.792	1.970	0.049	[0.01, 3.11]
d2	2.044	0.767	2.666	0.008	[0.54, 3.55]
d3	2.866	0.744	3.853	<0.001	[1.41, 4.32]
d4	3.160	0.740	4.273	<0.001	[1.71, 4.61]
d1 × Transparent	0.395	1.104	0.357	0.721	[-1.77, 2.56]
d2 × Transparent	0.664	1.069	0.621	0.535	[-1.43, 2.76]
d3 × Transparent	0.686	1.045	0.656	0.512	[-1.36, 2.73]
d4 × Transparent	0.517	1.042	0.496	0.620	[-1.53, 2.56]
Log-likelihood			-281.02		
Deviance			413.76		
Pearson Chi²			408		
Binomial family with logit link			(N = 135, Pseudo R² = 0.687)		

Table 2: **Generalized Linear Model Results**: Logistic regression analysis confirmed significant learning effects across all sessions, but no effect of barrier type or barrier × session interaction. Coef: Coefficient. SE: Standard error. Z:Z-statistics. CI: Confidence Interval.

We then investigated how many mice we would need to reproduce the findings from the current literature. To give an intuitive measure of the statistical power of our experimental design, we conducted a simulation-based power analysis to determine the sample sizes required to detect the significance level that previous studies reported for the barrier type × session interaction. Using our observed effect sizes and variance estimates from the mixed-effects model, we simulated datasets with increasing numbers of animal pairs per condition. At our current sample size (13 pairs for opaque condition, 14 pairs for transparent condition), we achieved approximately 20% power to detect a significant barrier × session interaction. To reach conventional power thresholds, we would require substantially larger sample sizes: approximately 30 mice pairs per condition for 80% power, and 50 pairs per condition for 95% power (Extended Data Fig. 1C).

Collectively, these results do not support the hypothesis that alloparental pup retrieval requires social transmission [6]. The consistently high performance rates in both barrier conditions — along with the absence of correlation between maternal and virgin performance — indicate that social transmission is not necessary for pup-naive females to acquire this behavior. Instead, the results suggest that virgin female mice possess latent, intrinsic capacities for alloparental behaviors that direct exposure to pups alone can activate.

Mother and virgins differ in the latency to initiate retrieval, not behavior execution

Under the latent behavior hypothesis, we would expect the different components of the behavior (initiation and execution) to be expressed differently. If pup retrieval is a latent behavior in mice, then this would mean that once a pup is picked up (i.e., the behavior is triggered), the animal should complete it (returning it to the nest). However, because the behavior is latent, it might require exposure to be triggered. Thus, we expect that the main difference between naive and expert animals on this task should consist at the level of initiating the behavior (identifying a distressed pup and reaching it). Thus, we split the total trial duration, defined as the time the animal displaces the pup from the nest until it returns it to the nest, in two: "reach pup latency" and "return pup latency". These two latencies reflect the time between pup displacement until the animal reaches the pup, and the time until the animal brings it back to the nest (Fig. 2). To test whether naive and expert animals differ specifically in initiating pup retrieval, we performed a linear mixed-effects model on reach and return latencies, including both mothers and virgin females across all sessions (Table 3).

We analyzed "reach" and "return" pup latencies using linear mixed-effects models (REML), including animal identity as a random effect to account for repeated measures. Fixed effects included group (mother vs. virgin), barrier type (opaque vs. transparent), session (d1–d4, relative to baseline d0), and their interactions. For this analysis, we pooled mother and virgin groups across barrier types when examining group differences, unless otherwise noted. For "reach pup latency", virgins were significantly slower than mothers, taking on average 3.4 times longer to reach a pup (group effect: $\exp(\beta = 1.231) = 3.4$, $p < 0.001$, Table 3). Barrier transparency did not have a significant effect ($\beta = -0.234$, $p = 0.131$), and the group $\times$ barrier interaction was not significant ($\beta = -0.207$, $p = 0.447$). Both mothers and virgins showed significant improvement over sessions: latency decreased by 17% on day 1 ($p = 0.049$) and 51% by day 4 ($p < 0.001$) relative to d0.

In contrast, "return pup latency" did not differ between mothers and virgins (group effect: $\beta = 0.244$, $p = 0.134$), nor did barrier type affect it ($\beta = 0.128$, $p = 0.297$) or the group $\times$ barrier interaction affect it ($\beta = 0.291$, $p = 0.179$). We observed a marginal decrease in return latency on day 3 ($p = 0.056$), with no other session effects reaching significance. Improvements in reach latency mirrored overall performance gains, with virgins showing significant increases in successful pup retrievals on day 3 ($\beta = 20.00$, $p = 0.004$) and day 4 ($\beta = 25.39$, $p < 0.001$) relative to d0 (Fig. 1C and 2, Table 3).

These findings indicate that the behavioral bottleneck in pup retrieval acquisition is not the motor execution of carrying pups but rather the decision-making and motivation process that initiates the retrieval behavior. This pattern was consistent across both transparent and opaque barrier conditions, and even in the mother groups, which further challenges the notion of any kind of social transmission facilitating the behavior.

	Reach Latency				Return Latency			
Effect	**Coef.**	**SE**	**Z**	**p**	**Coef.**	**SE**	**Z**	**p**
Intercept	2.68	0.13	20.83	<0.001	0.980	0.10	9.63	<0.001
Virgin	1.23	0.20	6.02	<0.001	0.244	0.163	1.50	0.13
Transparent	-0.23	0.155	-1.51	0.131	0.128	0.12	1.04	0.297
d1	-0.19	0.1	-1.97	0.049	-0.110	0.076	-1.43	0.15
d2	-0.41	0.1	-4.28	<0.001	-0.082	0.075	-1.08	0.28
d3	-0.5	0.09	-5.28	<0.001	-0.141	0.074	-1.91	0.06
d4	-0.72	0.09	-7.77	<0.001	-0.086	0.072	-1.19	0.23
Virgin×Transparent	-0.20	0.27	-0.76	0.447	0.29	0.21	1.35	0.179
Model Fit								
N (observations)	1273				1261			
Groups	48				48			
Log-likelihood	-1862.16				-1522.84			
Group Variance	0.130				0.082			

Table 3: **Mixed-effects analysis of latency components during successful pup retrieval.** Models analyzed log-transformed **A**. return latency and **B**. reach latency with fixed effects for group, barrier condition, session, and their interaction, plus random effects for individual animals. Virgin mice took significantly longer to reach pups ($\exp(1.231) = 3.4 \times$ slower, $p < 0.001$) but showed similar return speeds to mothers. Significant learning occurred in reach latency (sessions d1-d4 all $p < 0.049$) but not return latency. No barrier transparency effects were observed.

Discussion

Our study investigated whether social observation of maternal pup retrieval behavior leads to learning in virgin female mice. We tested virgin females who had never had any exposure to pups under transparent versus opaque barrier conditions while mothers demonstrated the pup retrieval task. Virgin females demonstrated robust acquisition of pup retrieval behavior regardless of barrier transparency. Around 85.7% of animals learned the behavior in the transparent condition and 76.9% in the opaque condition, with no significant difference between the groups (Fig.1). Correlation of maternal performance of pup retrieval and virgin performance was weak and non-significant, suggesting that maternal demonstration was not necessary for learning. Additionally, survival analysis revealed no difference between the two groups in the timing of behavior acquisition. Further, our virgins (in both barrier conditions) retrieved a pup as early as d0, differing from existing literature [6]. Circa 20% of all prescreened virgins retrieved 1 or more pups at d0, in contrast to less than 5% in the Carcea et al. study [6]. Thus, we accepted virgins that retrieved 1 pup or less at d0 in our cohorts.

To distinguish between behavior initiation and execution, detailed latency analysis revealed that group differences centered on the initiation phase of the behavior. Virgins in both conditions took longer to reach the pups when compared to mothers, but showed no difference in latency to return the pup to the nest. However, our latency analysis was constrained by the lower success rates in virgins, as they succeeded on fewer trials than mothers (535 successful trials for mothers in transparent condition, 524 trials for mothers in opaque condition; 126 successful trials for virgins in transparent condition, 88 for virgins in opaque condition).

The observation that virgins and mothers showed no significant difference in "return pup latency" once they picked up the pup suggests that the motor and motivational components of pup transport are already present in naive females. This finding indicates that the behavioral "program" for pup retrieval is genetically encoded but remains latent until hormonal triggers or pup exposure. Mothers, primed by hormonal changes and experience, present heightened attention to pup-related stimuli and stronger motivation to respond to pup distress signals [5, 7]. In contrast, virgins may initially require more time to process these signals and initiate appropriate responses. The improvement in performance across sessions suggests that repeated exposure to pups overcomes this attentional/motivational bottleneck.

Further work should thus disentangle the specific sensory pathways that can trigger maternal behavior. Pup odors and ultrasonic vocalizations provide powerful sensory cues that can trigger maternal responses in virgin females [8]. These olfactory and auditory stimuli may activate latent neural circuits associated with maternal care, even in the absence of visual observation. The similar acquisition rates between transparent and opaque barrier conditions suggest that these non-visual sensory cues might be sufficient to elicit maternal behavior.

Our results challenge the notion that virgins reliably socially transmit pup retrieval behavior. Carcea et al. [6] previously reported that 63% of non-co-housed virgins acquired pup retrieval through a transparent barrier, whereas only 11% learned through an opaque barrier. In contrast, we observed high rates of ac-

quisition under both conditions—78.6% for the transparent barrier and 76.9% for the opaque barrier—with no significant difference between them. To prevent any non-experimental exposure to pup cues, mothers and virgins were housed in separate rooms throughout the study, similar to the protocol that Carcea et al. described, which minimized the possibility that virgins were "primed" by pup odors outside of the task.

A post hoc power analysis reveals that our experiments would require over 30 animals per condition to reproduce the effect sizes that Carcea et al. reported, which constitutes far more animals than were used in both studies. While we closely followed the original protocol, subtle differences in experimental implementation—such as housing conditions, lighting, noise levels, or handling procedures—could have contributed to variability in behavior. If so, this would indicate that the pup retrieval task is highly sensitive to environmental and procedural factors, making replication across laboratories difficult. Taken together, these results suggest that social transmission of pup retrieval may be less robust than previously reported, and that researchers should interpret conclusions drawn from small-sample studies with caution.

Despite our findings, we should acknowledge some limitations. Our study focused on behavioral measures alone, without the direct assessment of neural activity, genetic differences, or hormonal states. While our results strongly suggest that virgin females can acquire maternal behavior independent of visual observation, we cannot directly determine the underlying neural mechanisms. The pattern of substantially different "reach pup latencies" but intact "return pup latencies" supports the hypothesis that maternal behaviors exist as latent neural programs that direct pup exposure can trigger, independent of social observation. Future studies incorporating neural recordings or manipulations will provide valuable insights into the mechanisms underlying this behavioral plasticity.

Methods

Animals

The Cantonal Veterinary Office Zurich, Switzerland, approved all animal procedures and experiments. All experiments used female C57Bl6/Crl1 mice (Jackson Lab) aged between 7 to 22 weeks at the start of the behavioral experiment. Animals were group-housed (around 2-4 litter-mates) in individually-ventilated cages (IVC) in a 12 h light/dark cycle room, and we provided them with food and water *ad libitum*. The subjects fell into two groups: dams (either primiparous or multiparous at the start of the experiment) and sexually- and pup-naive females (virgins), which were housed separately. Virgins were generated in-house, and we transferred them to a different pup- and breeding-free room upon weaning to avoid exposure to other pups and breedings. Virgins remained male-naive throughout the experiments. Dams and virgins were prescreened ("day zero", d0) for retrieval and pup mauling before initiating the behavioral task. We only accepted those virgins that retrieved 1 pup or less on d0.

Behavioral task

The established pup retrieval task [6] consists of two consecutive stages, 'demonstration' and 'testing', which we repeated over 4 days after prescreening (P1-4 of mother's pups). During the 'demonstration' phase, the dam and the virgin were placed on opposite sides of a conventional 1800 cm^2 home cage (588 mm $\times$ 194 mm $\times$ 395 mm, NexGen IVC for rats 1800, Allentown), and an opaque or transparent barrier separated them at the midline. We gave the animals 20 minutes to acclimatize before each demonstration session began. The dam's entire litter was grouped in a corner of the arena on the dam's side, and we covered them with nesting material. After an additional 1–2 minutes of acclimatization, we removed one pup from the nest and pseudorandomly placed it in either of the 3 other corners of the dam's cage partition, and we gave the dam a maximum of 2 minutes and 5 seconds to retrieve the displaced pup back to the nest. After 10 trials, the animals returned to their home cage, and a 30-minute break followed. We changed the used cage into a new, clean cage, and we placed the virgin on one of the partitions of the arena. After 20 minutes of acclimatization, the 'testing' phase began, and we put the entire litter back into the corner of the testing arena, covering them with nesting material. After 1–2 minutes of acclimatization, we tested the virgin for pup retrieval in 10 trials, as we described above. At the end of the experiment, all the animals returned to their home cages. We applied two different conditions of this task: 'transparent barrier', where the barrier dividing the cage was transparent (and therefore the virgins could observe the dam) and an 'opaque' condition, which consequently impeded the virgin from observing the dam and litter.

Behavioral analysis

A top view B/W CMOS camera (60516, Stoelting Europe) integrated with an ANY-maze system (Stoelting Europe) recorded all mouse behavior. The following parameters were quantified for analysis: **Reach pup latency**: the time to approach the pup ending in a pick-up, from pup displacement from the nest to the pick-up. **Return pup latency**: the time to retrieve the pup to the nest, from pick-up to return to the nest. **Total latency**: the whole trial duration, which is the sum of reach pup latency and return pup latency. **Retrieval success**: we categorized a trial as 'successful' if the female (mother/virgin) brought the pup back to the nest within the time allotted (maximum 2 minutes and 5 seconds), and 'failed' otherwise (the experimenter then returned the pup back to the nest at the end of the allotted time).

Statistical analysis

We analyzed retrieval performance at the trial level (success = 1, failure = 0) and retrieval latencies using custom Python scripts combining parametric and mixed-effects modeling approaches. To assess the effect of barrier conditions on virgin performance across days, and given the repeated-measures structure of the data, we applied linear mixed-effects models (LMMs) fit using restricted maximum likelihood estimation (REML) to examine the effects of barrier type, session, and their interaction on both success rates and

log-transformed latencies. In these models, we included pair IDs (for success rates) or the individual subject (for latency) as a random intercept to account for repeated measures, while fixed effects included group (mother vs. virgin), barrier, session, and relevant interactions. We additionally modeled trial-level outcomes using a binomial generalized linear model (GLM), with the number of successful and unsuccessful trials as the response variable. To follow approaches from previous studies [6], we additionally conducted a two-way ANOVA on the average success rates of animals in both barrier types.

To assess the robustness of our findings, we conducted a simulation-based power analysis using the fixed- and random-effects estimates from the fitted LMMs. For this, we generated simulated datasets under the alternative hypothesis with varying numbers of animals per condition, and the same REML-based mixed-effects model analyzed each dataset. The proportion of simulations yielding significant interaction terms ($\alpha = 0.05$) estimated statistical power, allowing us to determine the sample sizes required to detect effects of the magnitude that prior studies observed. Finally, we examined the relationship between maternal and virgin performance over days using Spearman correlation, to test whether maternal success predicted virgin acquisition within pairs.

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Figures

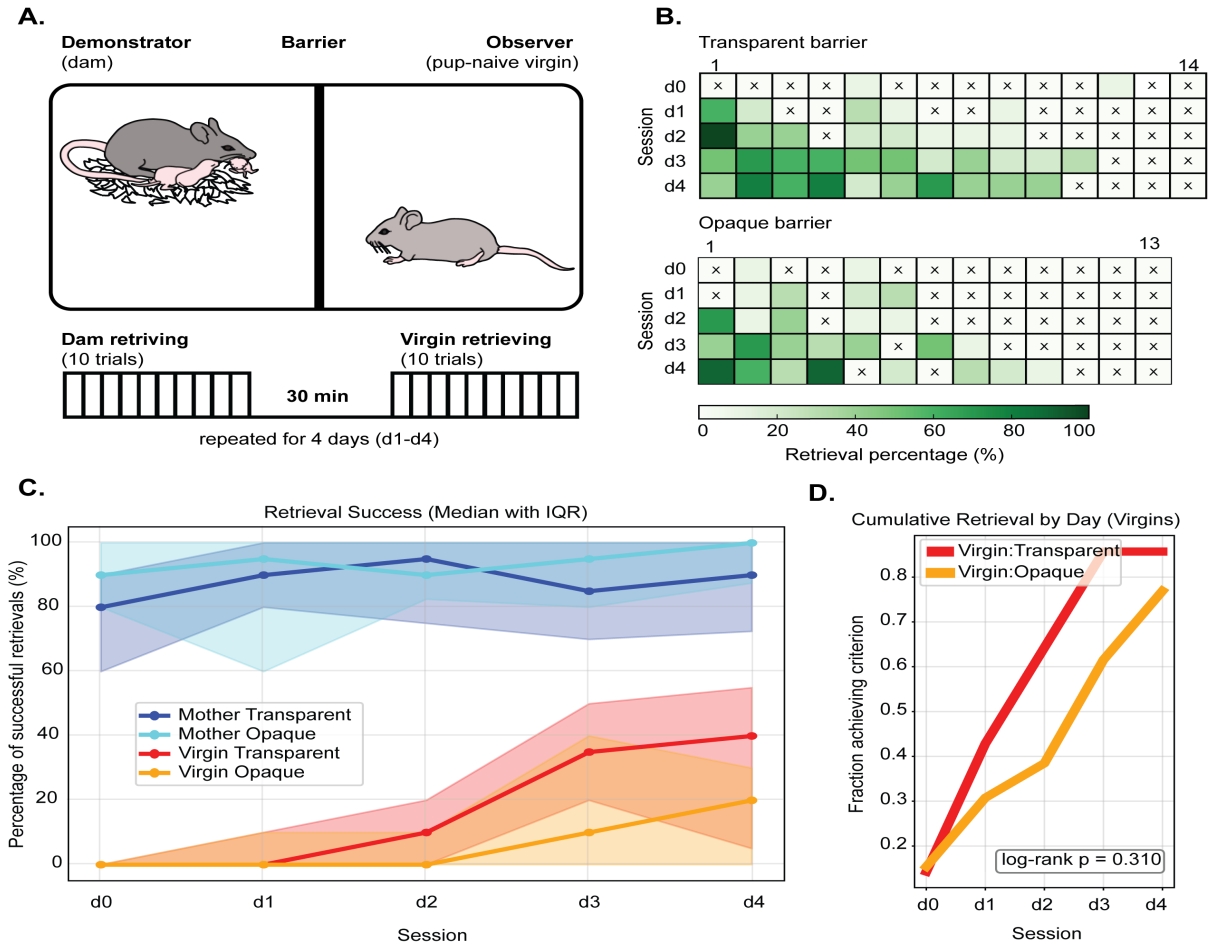

Figure 1: **Barrier condition on pup retrieval task does not influence virgin performance. A.** Task schematic of pup retrieval behavior task. A dam demonstrates pup retrieval for 10 trials, while a virgin observes through a transparent or opaque barrier. After a 30-minute break, the virgin is then tested for pup retrieval. The whole paradigm is repeated for 4 days. **B.** Heatmaps show virgin retrieval performance in transparent condition (top plot, $N = 14$ animals) and opaque condition (bottom plot, $N = 13$ animals). Dark green color = 100% retrieval rate; white color with 'X' mark = 0% retrieval rate. **C.** Lineplots depict successful retrievals over days (median with IQR) for each experimental group (Mother:Transparent in blue, Mother:Opaque in cyan, Virgin:Transparent in red, Virgin:Opaque in orange). **D.** Cumulative distributions (Kaplan-Meier) for retrieval onset in Virgins:Transparent (red) and Virgins:Opaque (orange). The log-rank test did not show any statistical significance rates between the two barrier conditions (log-rank $p = 0.310$).

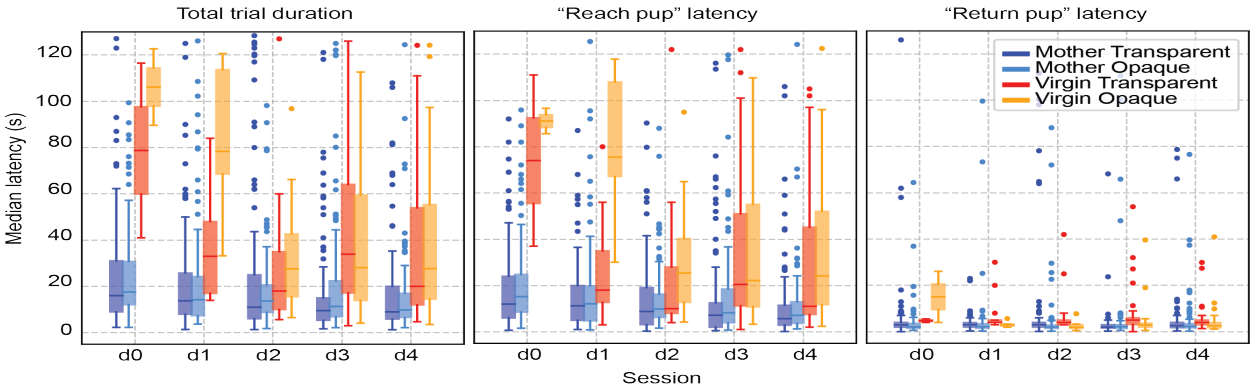

Figure 2: **Latency to reach the pup, but not latency to return the pup, differs between mothers and virgins.** Boxplots show median latency and IQR for **Left.** total trial duration, **Middle.** "reach pup latency" and **Right.** "return pup latency".