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# Evidence for cognitive plasticity during pregnancy via enhanced learning and memory

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**ABSTRACT**

Human and animal neuroscience studies support the view that plastic shifts occur in the brain during pregnancy that support the emergence of new maternal behaviours. The idea of adaptive plasticity in pregnancy is at odds with the notion of "baby brain", in which pregnant women describe the onset of forgetfulness. While inconsistent evidence for memory deficits during pregnancy has been reported, few studies have investigated spatial associative memory (which is consistently enhanced in studies of pregnant rodents). Moreover, most studies assess domain-general stimuli, which might miss adaptations specific to parent-relevant stimuli. In the present study, we examined the retention of spatial associative memory for parenting-relevant and non-parenting-relevant stimuli across 4-weeks in a sample of women in their third trimester of pregnancy, and compared their performance to a sample of never pregnant women. We demonstrated that relative to never pregnant women, pregnant women exhibited enhanced long-term retention of object-scene-location associations (spatial associative memory), as well as better initial learning about parenting-relevant, relative to non-parenting-relevant, stimuli. Thus, similar to studies in rodents, cognitive improvements were seen during pregnancy in humans, and those improvements were specific to the domain of spatial associative retention, and in the recognition of stimuli relevant to parenting.

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Pregnancy; associative memory; amnesia; baby brain

## Introduction

Neural plasticity is the ability of the brain to be shaped by experience and is the defining feature of the brain during the first decade of life (Galván, 2010; Nelson, 1999). While it is widely agreed that the high levels of experiential malleability characteristic of early development decrease dramatically with increasing age (Reh et al., 2020) resulting in an adult brain specialised for certain functions selected for during maturation, it remains possible that there are additional periods in adult life when child-like plasticity is once again momentarily observed. One such period may be the state of pregnancy in which massive changes occur within the female brain and body, helping to maintain the pregnancy and promote fetal growth, as well as facilitate the emergence of new maternal behaviours.

Across species, pregnancy is characterised by a mixture of biological, psychological, and cognitive shifts. For example, pregnant women experience dramatic hormonal changes (Brunton & Russell, 2008), alterations in neuroimmune signalling (Sherer et al., 2017), as well as adjustments in their anatomy and physiology (Moya et al., 2014), metabolism (Lain & Catalano, 2007), and even their microbiome composition (Koren et al., 2012). In humans, numerous studies have reported on the profound psychological changes that take place during pregnancy, including a reorientation towards the needs of the fetus and a revision of life goals and roles (Darvill et al., 2010; Leifer, 1977). Accompanying those shifts are large changes to brain anatomy and function. For instance, using anatomical correlates of brain age, the experience of pregnancy has been associated with younger brain age estimates in the immediate postpartum (Luders et al., 2018), which may persist many years into the middle life period (Lange et al., 2019; Ning et al., 2020). Pregnancy has also been associated with structural changes in grey matter volume, with such changes being associated with maternal-infant attachment in the postpartum (Hoekzema et al., 2017). Similarly, volume

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reductions have been observed in the ventral striatum during pregnancy (Hoekzema et al., 2020), and such reductions were associated with increased maternal responsiveness to infant cues in the postpartum period. As such the human neuroscience literature clearly supports the view that the brain changes that occur during pregnancy are functionally adaptive, favouring the mother in the care of her offspring.

Similar to human neuroscience studies, the rodent literature also supports the notion of a pregnancy-plasticity period, which functions to facilitate the emergence of new maternal behaviours. For example, compared to nulliparous or not pregnant rats, parous or pregnant rats exhibit improvements in spatial learning and memory (Love et al., 2005; Pawluski et al., 2006), object recognition and object placement (Macbeth et al., 2008a, 2008b; Paris & Frye, 2008), predation (Kinsley et al., 2014), and foraging behaviour (Lambert et al., 2005). These changes are accompanied by alterations in several neural regions, including structural and functional changes to the hippocampus (Macbeth et al., 2008b). Indeed, hippocampal morphological changes associated with pregnancy have been consistently reported in rodents (Eid et al., 2019; Pawluski & Galea, 2006; Wan et al., 2019), and immunological and hormonal changes endemic to pregnancy have been tied to hippocampal long term potentiation (LTP), as well as to hippocampal-dependent spatial learning and memory enhancements in pregnant females (Eid et al., 2019; Tomizawa et al., 2003). To date in rodent research, pregnancy appears to be associated with a host of brain and behavioural changes (particularly improvements in hippocampal-dependent spatial associative learning and memory) that would stand to benefit the new mother in the care of her infant (that is, that would assist the mother in tasks of, for example, foraging, hunting, and remembering nesting locations).

Interestingly, although some plasticity changes reported in pregnant humans are considered adaptive, e.g., those brain changes associated with subsequent mother-infant attachment (Hoekzema et al., 2017), at least in the domain of cognitive functioning, most reports in pregnant women are of impairments, or no change, in functioning. For example, while empirical studies and meta-analyses have shown that most objective memory and attentional functions appear to be largely unaffected by the experience of pregnancy (Christensen et al., 2010; Henry & Rendell, 2007), the performance of pregnant women on two task types, Verbal Paired Associates and tasks involving free recall, have consistently been shown to be impaired (Glynn, 2012; Henry & Rendell, 2007). Notably, these tasks tap different cognitive functions than those known to be enhanced in pregnant rodents, such as spatial and associative learning and memory (Lambert et al., 2005; Love et al., 2005; Macbeth et al., 2008b; Paris & Frye, 2008; Pawluski et al., 2006). Moreover, they each rely heavily on effortful processing and executive functioning networks, and less on intact hippocampal function (Clark et al., 2018; Henry & Rendell, 2007). It remains possible then that the period of pregnancy in humans, similar to that in rodents, is associated with enhanced cognition, but specifically for hippocampus-dependent spatial and associative learning tasks.

While minimal negative effects of pregnancy on cognitive functioning have been reported in humans, it remains true that pregnant women consistently complain of subjective memory deficits (Brindle et al., 1991; Logan et al., 2014; Parsons & Redman, 1991). In fact, this complaint is so frequently cited that it has come to be known colloquially as "pregnancy brain", "mommy brain", "baby brain", or "pregnancy amnesia" (Hurt, 2011; Shin et al., 2018). This discrepancy between objective and subjective reports of memory during pregnancy suggests that the oft cited "pregnancy brain" may actually be capturing processes adjacent to associative memory itself, e.g., shifts in attention away from the everyday and towards more ecologically relevant stimuli and tasks. Indeed, objective tests of memory (e.g., Verbal Paired Associates), rarely use stimuli that are ecologically relevant to the experience of parenting. Thus, it is possible that reports of objective memory deficits on certain tasks may be simultaneously missing boosts in memory performance on the same tasks for ecologically relevant, and therefore, attention grabbing stimuli. In other words, it is critical that future tests of cognitive functioning in pregnant humans include stimuli with ecological relevance to the experience of pregnancy and motherhood.

In the current longitudinal study, we compared the performance of pregnant and never pregnant women on the learning and long-term (4-week) retention of a spatial associative task which has been directly related to hippocampal functional activity patterns (Callaghan et al., 2021). We edited this task to include a comparison between two different stimuli types, one of which held ecological relevance for the experiences of pregnancy and motherhood (baby stimuli), and one of which held ecological relevance for the experiences of everyday adult life (adult stimuli). We assessed two types of recognition memory in this task which differed in their relative reliance on hippocampal function: (1) object-recognition memory (identifying whether objects had been seen before, which is relatively less hippocampus dependent) and (2) object-scene associative recognition memory (identifying correct pairs of objects and scenes from the task, which is associative and, therefore, relatively more hippocampus dependent) (Barker & Warburton, 2011; Callaghan et al., 2021). We hypothesised that pregnant women would either show evidence for attentional reorienting (reflected as better performance on the baby than adult stimuli) and/or evidence for a general cognitive enhancement (better performance than never pregnant women on both stimuli types) for the hippocampus-dependent associative memory task. Pregnant women were assessed in their 3rd trimester, as this is the stage

where the most pronounced changes in cognitive functioning have been observed (Christensen et al., 2010; Glynn, 2012).

## Materials and methods

### *Participants*

The sample included in these analyses were collected in two separate studies. The first study was in-person, and data were collected in our lab at Columbia University Irving Medical Centre. The sample for this study at enrolment was N = 74 women who were 32 weeks pregnant (Wave 1; mean age = 28.92 years, N = 17 with their first child), of whom N = 52 returned for the follow-up session when they were 36 weeks pregnant (Wave 2). In addition, N = 9 (mean age = 31.57 years) nulliparous women attended a Wave 1 in-person session (but were not asked to come in again for a follow-up visit due to the implementation of in-person research restrictions due to COVID-19). After COVID-19 prevented in-person data collection, another sample of N = 79 nulliparous women (mean age = 30.56 years) completed Wave 1 of the study online (using Cloud Research Services), of whom N = 60 also completed Wave 2, 4-weeks after Wave 1. See Table 2 for demographic information stratified by study. Importantly, to achieve a similar rate of follow-up for the online study to the in-person study, we invited online study participants back to complete Wave 2 in the order they completed Wave 1 until 60 participants had completed Wave 2, and then stopped (i.e., 23% attrition for the in-person study and 25% attrition for the online study. Attrition was not associated with demographic variables: age (lost to follow-up mean = 29.41 years, follow-up mean = 30.49 years, $t(79) = -0.57$, $p = 0.570$), income ($\chi^2(3) = 1.17$, $p = 0.758$), education ($\chi^2(3) = 3.78$, $p = 0.286$), depressive symptoms (lost to follow-up mean = 8.83, follow-up mean = 8.63, $t(93.23) = .19$, $p = .852$), ethnicity, ($\chi^2(1) = 0.30$, $p$ .568), and race ($\chi^2(1) = 0.463$, $p = .496$. Combining both studies together, the final sample for the pregnant women was N = 74 at Wave 1, and N = 52 at Wave 2, whereas the final sample for the nulliparous women was N = 88 at Wave 1, and N = 60 at Wave 2.

Considering the different methods of recruitment for the in-person vs. online study, and the fact that only the online sample was collected during the COVID-19 pandemic, we performed several different demographic comparisons (age, ethnicity, race, income, education, and depression symptoms) between data collected from the nulliparous women in-person vs. online before collapsing them into one group. The sample of nulliparous women collected in-person was not different from that collected online on the variables of age (online mean = 30.56 years, in-person mean = 31.57 years, $t(9.47) = 0.40$, $p = 0.701$), income ($\chi^2(3) = 0.91$, $p = 0.822$), education ($\chi^2(3) = 2.19$, $p = 0.534$), and depressive symptoms (online mean = 12.46, in-person mean = 7.89, $t(10.17) = -2.17$, $p = 0.055$). However, the nulliparous women whose data were collected in-person versus online were more likely to be Hispanic, $\chi^2(1) = 11.63$, $p < 0.001$, and were more likely to be non-White, $\chi^2(1) = 8.81$, $p = 0.003$. Considering the majority of demographic variables did not differ between these two nulliparous groups, they were collapsed into one nulliparous (never pregnant) group for subsequent analyses.

To characterise the demographic differences between the collapsed nulliparous group (collected in-person and online) to the pregnant group (all collected in-person) we again examined group differences in age, ethnicity, race, income, education, and depression symptoms. There was no difference between pregnant (M = 28.92 years) and nulliparous (M = 30.67 years) women in age, $t(159) = 1.86$, $p = 0.065$. However, the sample of pregnant women were more likely to identify as Hispanic than the women from the nulliparous group, $\chi^2(1) = 43.67$, $p < .001$, were more likely to identify as non-White race, $\chi^2(1) = 45.26$, $p < .001$, and also had different distributions of income, $\chi^2(3) = 13.95$, $p = 0.003$, and education levels, $\chi^2(3) = 22.72$, $p < 0.001$ (see Table 1). In addition, the pregnant group (M = 4.4) had lower levels of depressive symptoms than the nulliparous group (M = 11.99), $t(142.16) = 9.30$, $p < 0.001$. As such we used the variables of ethnicity, income, education, and depressive symptoms as covariates in the subsequent analyses. Although there were no age differences between the never pregnant and pregnant groups, as there was a wide distribution of ages in both groups in this study (18-45 years) we also decided to covary for the effects of age in the analyses. To ensure that the outcomes of the analyses were not dependent on the set of covariates chosen here, we repeated all analyses removing all of these demographic covariates and present those analyses in the Supplemental Results section (Tables S33-42). The results were largely similar with and without covariates included.

The data from the pregnant group presented in this paper were collected from women who were taking part in an ongoing Randomised Control Trial (RCT) in our lab at Columbia University Irving Medical Centre. The design of the RCT was to examine the effect of a brief relaxation intervention during pregnancy on mother-baby bonding. As the RCT was not related to the questions of interest for this study, it will not be discussed further here. However, to ensure that group assignment in the RCT did not influence performance on the memory task assessed in this paper, we tested the association between group assignment and memory performance within the pregnant group in a series of control analyses (see section "Statistical Analysis – Secondary (Control) Analyses' below for details).

All procedures for the in-person study were approved by the Institutional Review Board at Columbia University Irving Medical Centre. All procedures for the online study were approved by the Institutional Review Board at the University of California, Los Angeles.

**Table 1.** Demographic variables in each of the three samples included in this study.

| | Pregnant In-Person (N = 74) | Never Pregnant In-Person (N = 9) | Never Pregnant Online (N = 79) |
|---|---|---|---|
| Mean Age in years (range)‡ | 28.92 years (18-40 years) | 31.57 years (22-45 years) | 30.58 years (18-44 years) |
| Percent of sample who identified with race: * | | | |
| Asian American | 1.35% | 0% | 15.19% |
| African American/Black | 22.97% | 44.44% | 6.33% |
| White | 20.27% | 22.22% | 81.01% |
| Other↮ | 55.41% | 22.22% | n/a |
| Percent of sample who identified with ethnicity↧ * | | | |
| Hispanic | 67.57% | 55.55% | 10.13% |
| Not Hispanic | 32.43% | 33.33% | 89.87% |
| Percent of sample with education at each level: | | | |
| 12 years or less, equivalent of Elementary school or high school | 22.97% | 22.22% | 1.26% |
| 13–16 years, equivalent of vocational or technical school, associates degree, or an incomplete college degree | 52.70% | 44.44% | 8.86% |
| 17–18 years, equivalent of Bachelor's degree2 | 10.81% | 33.33% | 36.70% |
| > 18 years, equivalent of professional degrees or graduate level education | 13.51% | 0% | 53.16% |
| Percent of sample with income level: ↮ | | | |
| <$25,000 | 43.24% | 55.55% | 49.37% |
| $25,001 – $50,000 | 17.57% | 22.22% | 32.91% |
| $50,001 – $100,000 | 14.86% | 11.11% | 13.92% |
| >$101,000 | 20.27% | 0% | 3.79% |
| EPDS scores | | | |
| Mean depression score | 4.5 | 7.89 | 12.46 |
| Percent of sample with elevated depression levels | 0% | 44% | 52% |
| PSQI scores | | | |
| Mean PSQI score | 6.12 | n/a | n/a |

‡Missing data on 2 participants from the never pregnant online group.
* Missing data from 1 participant from the never pregnant in-person group.
↮The option "Other" was not available to the participants from the never pregnant online group. Participants could only select one racial category.
↧Missing data on 1 participant from the never pregnant online group.
↮Missing data on 3 participants from the pregnant group, and 1 participant from the never pregnant in-person group.

## Procedure

### *In-person study (pregnant group)*

Participants for the in-person study completed two in-person visits to our lab at Columbia University Irving Medical Centre. In the first visit (Wave 1, 32 weeks of pregnancy), participants completed a range of questionnaires (some of which are reported in this paper – depression, sleep and demographic information), a relaxation intervention (depending on group assignment in the RCT), biospecimen collection, and a range of additional measures not discussed here. At the end of the session, participants completed the behavioural memory training task on a computer, followed by a memory test immediately after training (both of which are the focus of this study). The entire session took approximately 2-2.5 hours and participants were reimbursed $60 for their time (approximately $0.40 per minute). In the second visit (Wave 2, 36 weeks of pregnancy for the pregnant participants), participants again visited the lab for another 2-2.5 hour session, at the end of which they completed the long-term behavioural memory test on a computer. The long-term memory test was identical to the first memory test completed during Wave 1. Participants were reimbursed $70 (approximately $0.58 per minute) for their time at this second visit. The average time between Wave 1 and Wave 2 was 29 days (range 12–41 days).

### *In-person study (never pregnant group)*

Participants completed one visit to our lab at Columbia University Irving Medical Centre. These participants were not randomised into the relaxation intervention. At their in-person session they completed a range of questionnaires (some of which are reported in this paper – depression and demographic information), and additional measures not discussed here. At the end of the session, participants completed the behavioural memory training task on a computer, followed by a memory test immediately after training (both of which are the focus of this study). Their visit took approximately 2 hours to complete and they were reimbursed $50 for their time (approximately $0.41 per minute). This group was not invited to a second session because of the onset of in-person research restrictions due to the COVID-19 pandemic, and thus, their data are included only in the assessments of learning (i.e., immediate memory).

### *Online study (never pregnant group)*

Participants completed two online sessions via CloudResearch (a managed recruitment and research service which uses MTurk workers). Participants were screened for eligibility (18-45 years of age, female, nulliparous) through CloudResearch, and eligible participants were invited to complete Wave 1 of data collection until the

**Table 2.** Impact of COVID on Never Pregnant Online Group.

| Item from the COVID-19 Impact Questionnaire | Percent of Never Pregnant (Online) Sample Endorsing Question/Mean Scale Rating |
|---|---|
| COVID-19 positive or suspected – self | 2.53% |
| COVID-19 positive or suspected – other | 24.05% |
| COVID-19 known deaths – other | 3.80% |
| Lack of access to food/water/ medical care | 17.72% |
| Loss of personal or business income | 49.37% |
| Insurance coverage for financial loss (if applicable) | 9.52% |
| Living in a COVID-19 hotspot | |
| Yes | 15.19% |
| No | 64.55% |
| Don't Know | 20.25% |
| Separation from family | 29.11% |
| Isolation or quarantine | 31.65% |
| Change in living arrangement (e.g., residence or guests) | 6.33% |
| Change in employment | 44.30% |
| Mean COVID-19 distress rating, range "Not At All" to "Very Much" (5 point rating) | Mean = 3.25, range = 1-5 |
| Mean mental health impact rating, range "Not At All" to "Very Much" (5 point rating) | Mean = 3.41, range = 1-5 |
| Mean social support impact rating, range "Not At All" to "Very Much" (5 point rating) | Mean = 2.91, range = 1-5 |
| Global Impact of COVID-19 "Very Negative" to "Very Positive (5 point rating) | Mean = 2.33, range = 1-5 |

achieved target enrolment was reached. Once participants logged into the study, they were sent to a link to complete the study on the website Gorilla (www.gorilla.sc). Once the participant completed the study (approximately 25 minutes), they were directed back to CloudResearch to receive their payment ($4.20 for Wave 1, approximately $0.17 per minute). Exactly four weeks after completion of Wave 1, participants were invited to complete Wave 2 via an email from CloudResearch. After accepting the invitation, participants were directed back to Gorilla to complete the study (approximately 10 minutes), before then being redirected back to CloudResearch to receive their payment ($2.80 for Wave 2, approximately $0.28 per minute). We considered the lower payments per minute for completing the study online, relative to in-person, to be reasonable considering the simplicity of the online study. The average time between waves was 28 days (range 26–34 days), which was significantly shorter by three days than the average time between waves in the pregnant group (30 days), $t(48.96) = 2.10$, $p = .041$.

The online data were collected between September 8th and October 16th, 2020. In historical context, these dates were approximately 6 months after COVID-19 was declared a national emergency in the United States, and amid early vaccine trials.

## Questionnaires

### Demographics

All participants were asked to report on several demographic variables, including their age, race and ethnicity, education level, and income level. Descriptive statistics by each of the three groups (pregnant, never pregnant in-person, never pregnant online) are reported in Table 1. Demographic variables that differed between the pregnant and never pregnant (collapsed across in-person and online) groups were also used as covariates in the behavioural analyses as described above. In addition, pregnant women also reported on their parity (first pregnancy or multiparous). We examined whether parity was associated with memory performance within the pregnant group in secondary control analyses (as described below).

### Depression symptoms

The Edinburgh Postnatal Depression Scale (EPDS) (Cox et al., 1987) is a 10-item self-report questionnaire that asks participants to rate their mood across the last week and was used as an estimate of depressive symptoms for both pregnant and never pregnant participants in this study. Each item involves a statement and participants rate their agreement with each statement on a 4-point scale (0-3). After reverse scoring on three of the items, participants' scores are summed to create a total which ranges from 0-30. Scores above 12 are considered to be elevated and may indicate a depression diagnosis. For the pregnant and never pregnant samples collected in-person, all 10-items were administered. However, for the never pregnant sample collected online, as the study was anonymous, one item on self-harm was dropped because there was no way to follow-up and provide care for participants who reported self-harm intentions. Thus, for EPDS data collected online, the score for the dropped item was imputed as the mean of the answered items before the total score was summed.

### Sleep quality

The Pittsburgh Sleep Quality Index (PSQI) is a 19-item self-report questionnaire that asks participants questions about their quality of sleep in several domains, including time spent sleeping, disturbances in sleep, use of sleep aids and medications, and sleep quality (Buysse et al., 1989). Responses to the 9 items form 7 component scores, each of which range from 0–3 points ("3" being severe difficulty). Component scores are summed to create a global score ranging from 0–21 points, with higher scores indicating more difficulty in sleep quality. The PSQI was administered only to the pregnant participants and was used in secondary control analyses (as described below).

### COVID-19 impact

Never pregnant participants completing the study online were asked 21 questions about the impact that COVID-19 was having on their lives in the domains of positive tests or symptoms in self and others, deaths of close others, access to essentials (e.g., food, water, medical care), financial impact, employment impact, geographic impact (e.g., living in a hotspot), family separations, residential changes, household composition changes, distress and emotional wellbeing. Descriptive statistics for the items covered on this questionnaire are presented in Table 2. Participants' responses to one item concerning the global impact that COVID-19 was having on their lives (scored on a scale of 1 "very negative" to 5 "very positive") were used to test whether the impact of COVID-19, including and in addition to depressive symptoms, was associated with memory performance in the never pregnant group in secondary control analyses (as described below). Table 3

## Memory task

### Stimuli

The object stimuli for this study were taken from Google searches on the internet and were chosen as objects that one might encounter in everyday life if they were the parent of an infant (baby objects), or in an office environment (adult objects). Examples of baby objects included pictures of high chairs, infant clothing, bibs, and toys. Examples of adult objects included pictures of office chairs, office attire, stationary, and equipment (e.g., photocopier machine). Distractor stimuli fell into the same category as the target stimuli (adult and baby objects) but there were no overlapping exemplars within categories, e.g., if a high chair was a target, a different style of high chair was not used as a distractor.

Scene stimuli were also taken from Google searches on the internet and included a mixture of photographs of indoor and outdoor scenes. The scenes were selected to be engaging, but were relatively free of foreground items to ensure that the paired objects from the task would stand out over the scene background.

**Table 3.** Comparison of individuals with data exclusions vs. no data exclusions on key demographic variables.

| | Wave 1 | | Wave 2 | |
|---|---|---|---|---|
| | Object-recognition learning | Object-scene associative learning | Object-recognition memory | Object-scene associative memory |
| **Age** | $t(5.21) = .25$, $p = .816$ | $t(22.12) = .14$, $p = .887$ | $t(11.59) = .77$, $p = .459$ | $t(60.19) = 1.99$, $p = .052$ |
| **EPDS** | $t(5.55) = .26$, $p = .084$ | $t(21.13) = .09$, $p = .931$ | $t(13.87) = .85$, $p = .408$ | $t(49.34) = .98$, $p = .333$ |
| **Ethnicity** | $\chi^2(1) = 1.84$, $p = .175$ | $\chi^2(1) = .52$, $p = .470$ | **$\chi^2(1) = 5.50$, $p = .019$** | $\chi^2(1) = 2.08$, $p = .150$ |
| **Race** | $\chi^2(1) = 1.68$, $p = .195$ | $\chi^2(1) = 3.71$, $p = .054$ | $\chi^2(1) = .25$, $p = .615$ | $\chi^2(1) = 3.23$, $p = .570$ |
| **Income** | $\chi^2(3) = 2.39$, $p = .495$ | $\chi^2(3) = 4.37$, $p = .224$ | $\chi^2(3) = 1.66$, $p = .647$ | $\chi^2(3) = 1.37$, $p = .714$ |
| **Education** | $\chi^2(3) = 2.72$, $p = .437$ | $\chi^2(3) = 3.78$, $p = .286$ | **$\chi^2(3) = 9.21$, $p = .027$** | $\chi^2(3) = 5.91$, $p = .116$ |

People excluded from the object-recognition memory test at Wave 2 were more likely to be non-Hispanic than people who were included. They were also more likely to have a Bachelor's degree than people who were included (included people were more likely to have 13–16 years of schooling, such as a technical or vocational degree).

### Learning

Participants performed two blocks of learning which involved passive viewing of visual stimuli. The learning task consisted of 40 trials per block which were presented to participants via PsychoPy3 (in-person study) or Gorilla (online study). On each trial, a photograph of an indoor or outdoor scene appeared on the screen for 2000ms, and then an object appeared in one of four quadrants (upper left, upper right, lower left, lower right) of the screen, overlaid on top of the scene, and remained on screen for another 2000ms (see Figure 1 for a graphical representation of the memory task). Each trial was separated by a fixation cross which appeared in the middle of the screen for 1500 ms. In total there were 20 different objects presented in each block embedded in 10 scenes. Thus, each of the 10 scenes was paired with two objects, and each object was presented in a different quadrant of the scene. Each object was presented twice during the learning phase, each time in the same quadrant of the same scene, yielding a total of 40 trials per block. The objects presented within each block were from a similar category, and were different between blocks. For each participant, one block (adult block) included objects from an office environment (e.g., photocopier, stapler, office chair), and the other block (baby block) included baby-relevant objects (e.g., playmat, bottle, baby monitor). Within each block, stimuli were presented in a fixed random order. The starting block (adult or baby) was counterbalanced between participants. The whole learning task (both adult and baby blocks) took approximately 8 minutes to complete viewing (including instructions).

For the learning task, participants were told that they would be looking at objects in scenes, and they were asked to imagine the object in the scene in as much detail as possible. Each participant was then given an example trial (stimuli in the example trial were not repeated in the training set). After confirming that they understood the instructions, participants moved to the first learning block (adult/baby – order counterbalanced between participants). After the first learning block was completed, participants were given a short break (self-timed) and then moved to the final block of learning (baby/adult, whichever was not completed on the first block).

Due to the potential for higher rates of inattention in participants completing the study online, relative to in-person, we included eight attention check items into the

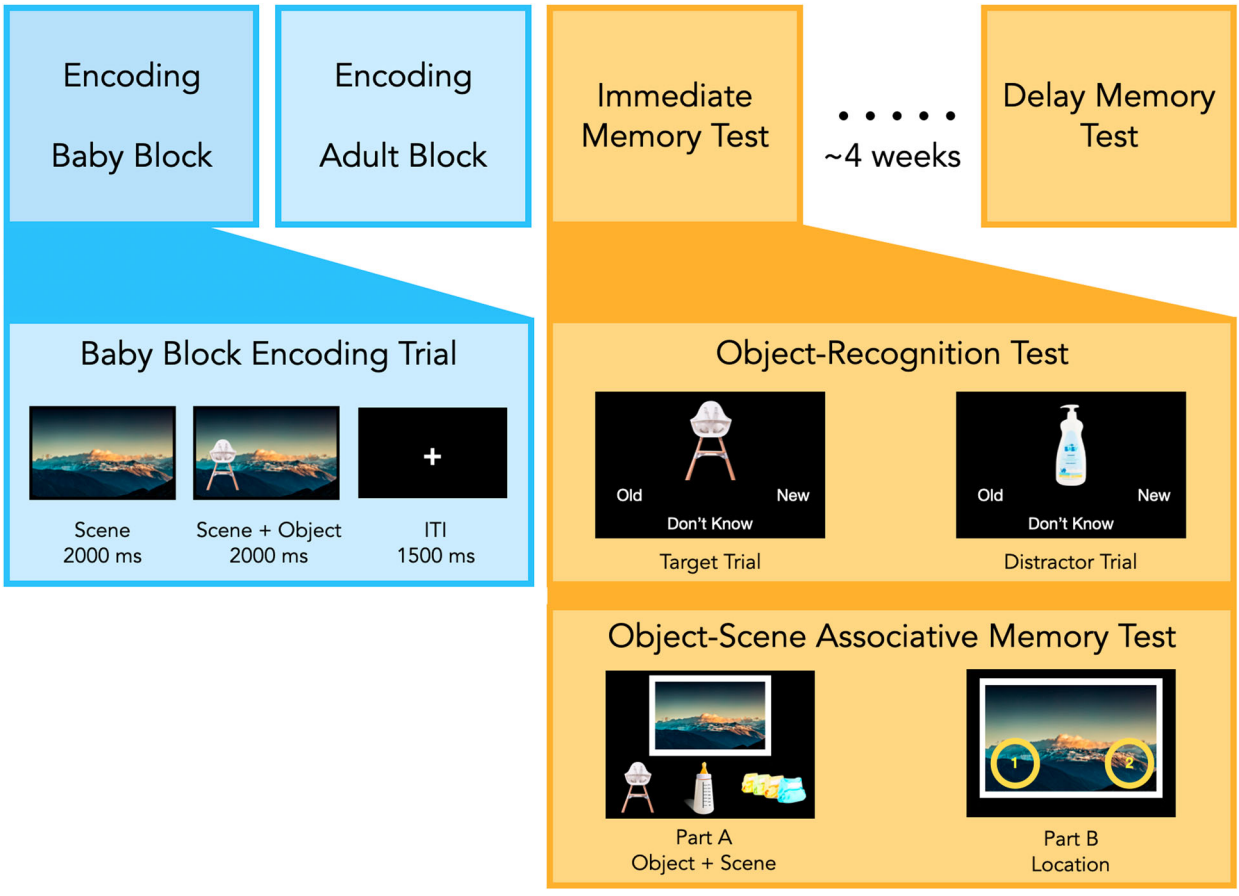


**Figure 1.** Depiction of the encoding and test portions of the memory task. Encoding (see blue panel to the left of the figure) consisted of two blocks, one with baby objects and the other with adult objects. Each block consisted of 40 trials (see enlarged panel below "Encoding Baby Block" as an example of a trial), in which a scene was presented on the screen for 2000ms, followed by the object appearing in the foreground of the scene for another 2000ms. Each trial was interspersed with an intertrial interval (ITI) of 1500 ms, during which a white cross was presented on a black background, before the next trial began. In the test phase, which occurred both immediately after learning and at a delay of approximately 4-weeks after learning participants were presented with two identical tests (see enlarged panel below "Immediate Test" as an example of what each test looked like). For the object-recognition test, participants were shown objects they had seen during encoding (targets) and new objects (distractors), and were asked to pick a response: "old", "new" or "don't know". After the object-recognition test, all participants then progressed to the object-scene associative memory test, in which they were first shown a scene from encoding with 3 target objects underneath, 1 of which had been paired with that scene during encoding (Part A). After choosing what object was paired with that scene, they then had to choose where it was located in the scene from two response options (Part B).

online training task. Attention checks involved showing participants two different shapes in two different colours and asking them to choose the correct shape or colour from two options. Performance on this attention check task was universally high (mean correct = 7.98, range 7-8), and thus we did not use performance on this measure as a covariate for analyses.

### *Test*

Participants performed two identical memory tests after completing the learning phase of the task. The first was performed immediately after the learning phase was completed (during Wave 1, immediate memory), and the second was completed during the Wave 2 session (approximately 4 weeks after Wave 1, delay memory; see Figure 1; NB: that the N = 9 never pregnant participants collected in-person only completed the test at Wave 1). The same stimuli were tested at the immediate and delay intervals; however, participants were not provided with feedback on whether their responses were correct during either the Wave 1 or the Wave 2 memory test.

Each memory test was self-paced and was divided into two sections: an object-recognition memory section (i.e., relatively less hippocampus-dependent), and an object-scene associative memory section (i.e., relatively more hippocampus-dependent) described in detail below.

#### *Object-recognition memory*

Participants were shown a single object in the top middle of the screen, and were given three response options below the object: "old", "new", "don't know". Participants were instructed to look at the object and to press "old" if they remembered seeing the object during the learning phase of the task, "new" if they did not remember seeing the object during the learning phase of the task, and "don't know" if they were not sure. Participants were presented with the 40 stimuli seen during the learning phase

(20 adult and 20 baby objects – targets) and 40 new stimuli which had not been presented during the learning phase, but were from the same categories as the learned stimuli (20 adult and 20 baby objects – distractors). The target and distractor stimuli were presented in a fixed random order in two continuous blocks (all adult targets and distractors followed by all baby targets and distractors). The order of the blocks was counterbalanced and participants received the counterbalancing order that matched the order they received during the learning phase (i.e., if baby trials were presented first during the learning phase, they were also presented first during the test). We calculated participants' hits (the proportion of targets correctly identified as "old") as well as their false alarms (the proportion of distractors incorrectly identified as "old"). We then calculated D-prime by converting hits (H) and false alarms (FA) to z-scores, and subtracting Z(FA) from Z(H) for each participant. In other words, D-prime is a measure of sensitivity that takes into account both hits and false alarms. Someone who says "old" to all items would have both a high hit rate and a high false alarm rate, but a low sen sensitivity rate (D-prime).

### *Object-scene associative memory*

After participants completed the object-recognition section of the test, they moved onto the object-scene associative memory section. In the first part of this test (Part A) participants saw a scene from the learning phase of the task with three objects underneath, and were asked to pick which object had been paired with the scene during the learning phase. Each of the objects was a target but only one of the objects had been paired with that particular scene during the learning phase of the task (i.e., was a correct pair). Once the participant made a response for Part A, they then moved onto Part B, where the scene remained on the screen, but the three objects underneath were removed, and participants were asked to indicate where the object had been located from a choice of two potential locations within the scene. When Part B was answered, participants moved to Part A for another trial. Participants answered Part A and B of the object-scene associative memory test for all 20 adult and 20 baby trials. We calculated performance accuracy based on two metrics both of which we expected to be hippocampus-dependent, but that varied in difficulty because of the detail of the memory required: "coarse episodic memory" was the proportion of correctly identified object-scene pairings in Part A (less detailed memory required), and "detailed episodic memory" was the proportion of trials where both Part A (the object + scene pairing) and Part B (the location) were correct (more detailed memory required). Chance performance for the coarse episodic memory metric was 33.33% as participants were choosing between three options. Chance performance for the detailed episodic memory metric was 16.67% (i.e., 33.33% * 50% for 2 potential locations).

We analysed all trials from the object-scene associative memory test, whether or not participants had correctly recognised the object as a target during the object-recognition portion of the test.

## Missing data and exclusions

### *Object-recognition memory (D-prime, hits and false alarms)*

Of the original N = 162 (N = 74 pregnant; N = 88 never pregnant) participants intended for analysis in Wave 1, N = 4 pregnant participants were missing data for the object-recognition portion of the memory test due to experimenter error. Thus, the resulting sample size with data for object-recognition memory at Wave 1 was N = 158 (N = 70 pregnant; N = 88 never pregnant) participants. Because of the potential for higher levels of inattention for participants completing the study online, relative to in-person, we excluded participants based on performance accuracy lower than chance levels (D-prime < = 0 for either the trials using adult or baby stimuli, indicating chance performance). This resulted in the exclusion of data from N = 6 participants from the never pregnant group and zero participants from the pregnant group (final analysed sample N = 152: N = 70 pregnant; N = 82 never pregnant). This difference in exclusion rates between the never pregnant and pregnant groups was expected as the majority of the never pregnant participants completed the task online, rather than in person.

Of the original N = 112 (N = 52 pregnant; N = 60 never pregnant) participants intended for Wave 2 analysis, N = 1 pregnant participant was missing data for the object-recognition portion of the memory test due to experimenter error. Thus, the sample size with data for object-recognition memory at Wave 2 was N = 111 (N = 51 pregnant; N = 60 never pregnant). Before analysis, N = 11 never pregnant participants were excluded based on low performance accuracy (D-prime < = 0) on either Wave 1 or Wave 2 trials, resulting in a final sample size of N = 100 (N = 51 pregnant; N = 49 never pregnant).

### *Object-scene associative memory (coarse and detailed memory metrics)*

Of the original N = 162 (N = 74 pregnant; N = 88 never pregnant) participants intended for Wave 1 analysis, N = 19 (N = 9 pregnant; N = 10 never pregnant) participants were excluded from the analysis based on low performance accuracy (< 33.33%, chance level performance on Part A of the object-scene associative memory test), resulting in a final sample size of N = 143 (N = 65 pregnant; N = 78 never pregnant). A comparison of individuals with missing data from those with complete data on key demographic variables is provided in Table 3.

Of the original N = 112 (N = 52 pregnant; N = 60 never pregnant) participants intended for Wave 2 analysis, N = 37 (N = 15 pregnant; N = 22 never pregnant) participants

were excluded from the analysis based on low performance accuracy (<33.33%, chance level performance on the item-scene association at either Wave 1 or Wave 2), resulting in a final sample size of N = 75 (N = 37 pregnant; N = 38 never pregnant).

## Statistical analysis

### Primary analyses

The data from the memory tests were analysed in a series of linear mixed-effects models, fit using Restricted Maximum Likelihood Estimates (REML), and with participant identity entered as a random effect using the "lmerTest" package in R (Kuznetsova et al., 2017). Type III Analysis of Variance Tables using Satterthwaite's Method for degrees of freedom were calculated on each linear mixed effect model using the "anova" function, which has been shown to produce accurate Type I error rates for REML linear mixed-effects models (Luke, 2017). Each model tested for the effect of group (binary coded – pregnant or never pregnant), stimuli (adult vs. baby stimuli), and the interaction between Group and Stimuli. Significant interactions were probed by comparing the estimated marginal means from the model using the "emmeans' package in R (Lenth, 2020). Beyond the effects of interest, each model also covaried for the effects of ethnicity (binary coded – Hispanic vs. not Hispanic), race (binary coded – White vs. Other Race), age (mean centred continuous), income (categorised), education (categorised), and summed scores on the Edinburgh Postnatal Depression Scale (EPDS, log transformed and mean centred). Each set of analyses was run once on the Wave 1 data to examine how pregnancy affects learning, and again on the Wave 2 data (controlling for performance at Wave 1) to determine how pregnancy affects delayed memory retention. Statistical significance was considered as an $\alpha$ value of less than 0.05.

### Secondary (control) analyses

In addition to the primary linear mixed-effects models just described, we also ran a series of secondary linear mixed-effects models for Wave 1 and Wave 2 data to test for effects of sleep quality, parity, and group membership within the RCT, on memory performance within the pregnant group, and to test for the effects of COVID-19 impact on memory performance in the never pregnant group (collected online). These models also included effects of stimuli (adult vs. baby stimuli). For Wave 2 data, Wave 1 performance was entered as a covariate. Tables presenting the results of these secondary linear mixed-effects models are presented in the supplemental results section that accompanies this manuscript.

## Results

The results from Wave 1 and 2 for each of the object-recognition and object-scene associative memory tests are summarised in Table 4.

**Table 4.** Summary of results for object-recognition and object-scene associative learning (Wave 1) and retention (Wave 2) memory.

| | | Learning (Wave 1) | Retention (Wave 2) |
|---|---|---|---|
| **Object-Recognition Memory** | Adult Objects | Pregnant = Never Pregnant | Pregnant = Never Pregnant |
| | Baby Objects | Pregnant > Never Pregnant | Pregnant = Never Pregnant |
| **Object-Scene Associative Memory** | Adult Objects | Pregnant = Never Pregnant | Pregnant > Never Pregnant |
| | Baby Objects | Pregnant = Never Pregnant | Pregnant > Never Pregnant |

## Learning (wave 1)

### Object-recognition memory

Using D-prime scores, there was a significant Group by Stimuli interaction, $F(1, 140) = 11.36$, $p = .001$, partial $\eta^2 = .08$, on object-recognition performance at Wave 1 (see Figure 2a). Post-hoc tests of the estimated marginal means indicated that memory for adult stimuli was similar in the pregnant and the never pregnant group, $t(155) = .15$, $p = .883$, d = -.02. However, there was an indication that memory for baby stimuli was higher in the pregnant group than the never pregnant group, with results trending towards significance, $t(155) = 1.96$, $p = .052$, d = -.31. When comparing memory for the different stimuli within groups, for the never pregnant group memory for adult stimuli was higher than for baby stimuli, $t(140) = 3.65$, $p = .001$, d = .31, but for the pregnant group memory for adult and baby stimuli did not differ, $t(140) = 1.24$, $p = .217$, d = -.10. Beyond the interaction effect, there was also a significant effect of age, whereby D-prime was higher in older than younger participants, $F(1, 134) = 7.97$, $p = .005$, partial $\eta^2 = .06$. No other main effects were significant (see supplemental Table S1). To break down the contribution of hits and false alarms to D-prime scores, we also ran the same analyses just described on hits and false alarms separately. For hits, there was a significant interaction between Group and Stimuli, $F(1, 140) = 14.70$, $p < .001$, partial $\eta^2 = .10$, (see Figure 2b), which was driven by higher hit rates to baby stimuli in the pregnant than in the never pregnant group, $t(186) = 2.61$, $p = .010$, d = .38, and greater hits to baby stimuli than to adult stimuli within the pregnant group, $t(140) = 4.09$, $p < .001$, d = .35 (Figure 2b). For false alarms, there was a main effect of stimuli, whereby false alarms were higher to baby than adult stimuli, $F(1, 140) = 26.59$, $p < .001$, partial $\eta^2 = .16$ (Figure 2c; see Supplemental Table S2-S3 for full results from hits and false alarm models).

### Control analyses for object-recognition memory

There were no associations between sleep quality, parity, or RCT experimental group, on D-prime, hit rate, or false alarm rates within the pregnant group (see supplemental Table

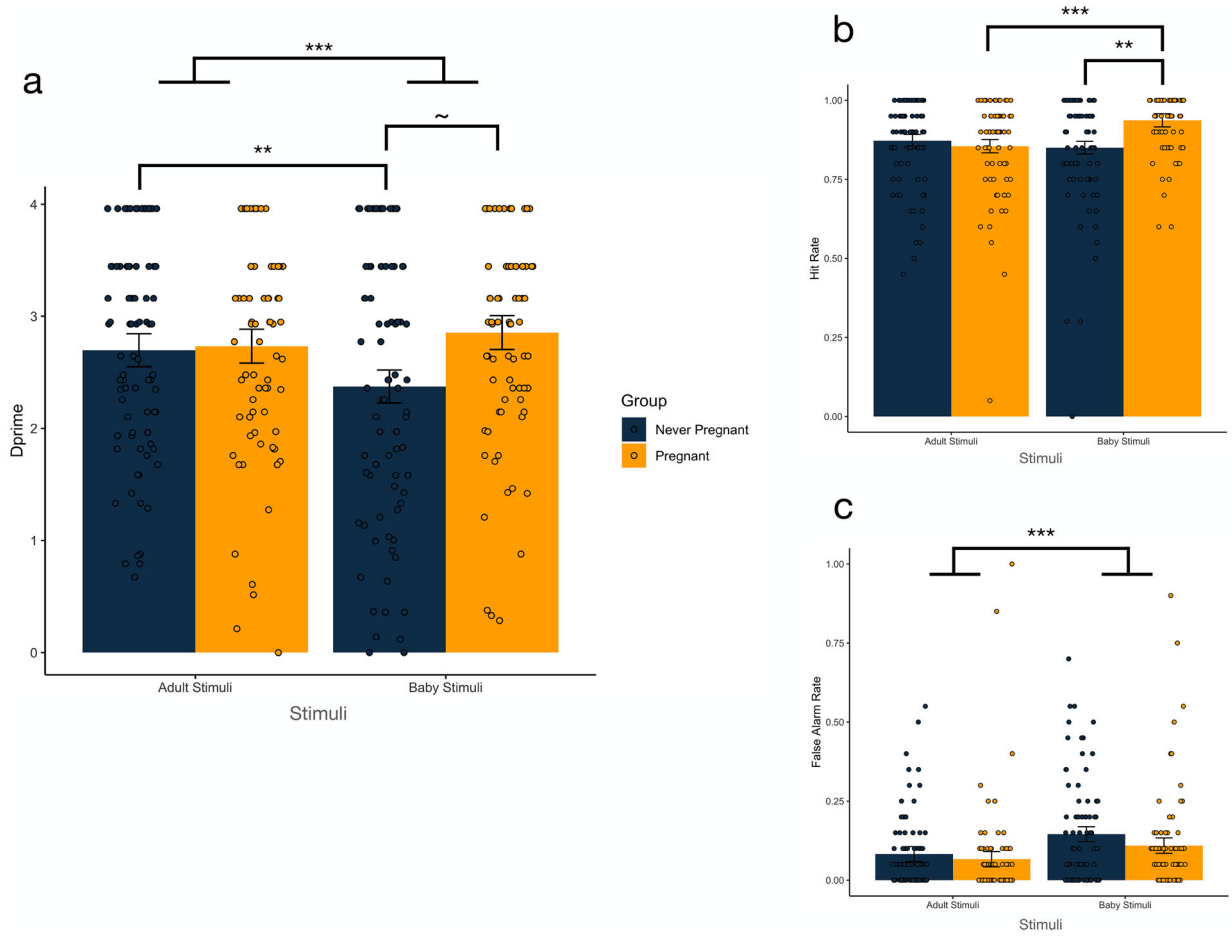


**Figure 2.** Object-Recognition Memory at Wave 1. Estimated marginal means from the linear mixed effects models assessing (a) D-prime, (b) Hit Rate, (c) False Alarm Rate, in pregnant (mustard) and never pregnant (navy) participants at Wave 1. Bars indicate the estimated marginal means from the models and the error bars reflect the standard error of those means. Individual participant raw data is plotted overlaid on the bars using dots (jittered along the x-axis for increased visibility of the individual data points). Responses to the adult stimuli from the task are represented in the two leftmost bars for each graph component, and responses to the baby stimuli from the task are represented in the two rightmost bars for each graph. Connecting lines with stars represent the significant contrasts and main effects. * $p < .05$, ** $p < .01$, *** $p < .001$, ~ $p = .052$ (trend effect).

S4a-i). There was also no association of COVID-19 impact scores on D-prime, hit rate, or false alarm rates within the never pregnant group (see supplemental Table S5a-c).

### *Object-scene associative memory*

For the coarse episodic memory index, there was an effect of trial type, whereby performance accuracy was higher to adult than baby stimuli, $F(1, 133) = 13.04$, $p < .001$, partial $\eta^2 = .09$ (see Figure 3a). There was also a significant effect of age whereby accuracy was higher in older than younger participants, $F(1, 127) = 6.60$, $p = .011$, partial $\eta^2 = .05$. No other main effects or interactions were significant (see supplemental Table S6).

For the detailed episodic memory index, there was an effect of age, whereby performance accuracy was higher in older than younger participants, $F(1, 127) = 5.54$, $p = .020$, partial $\eta^2 = .04$ (see Figure 3b). No other main effects or interactions were significant (see supplemental Table S7).

### *Control analyses for object-scene associative memory*

Within the pregnant group, there was an effect of parity on coarse episodic memory, $F(1, 63) = 5.62$, $p = .021$, partial $\eta^2 = .08$, and detailed episodic memory, $F(1, 63) = 4.27$, $p = .043$, partial $\eta^2 = .06$, whereby being a first-time mother was associated with greater accuracy than being a multiparous mother. However, no other associations between sleep quality or RCT experimental group were evident for coarse or detailed episodic memory at Wave 1 within the pregnant group (see supplemental tables S8a-f). Within the never pregnant group, there was no association between COVID-19 impact score on coarse or detailed episodic memory at Wave 1 (see supplemental Table S9a-b).

## Long-term memory (wave 2)

### *Object-recognition memory*

Using D-prime scores, there was an effect of stimuli, whereby D-prime to adult stimuli was higher than to

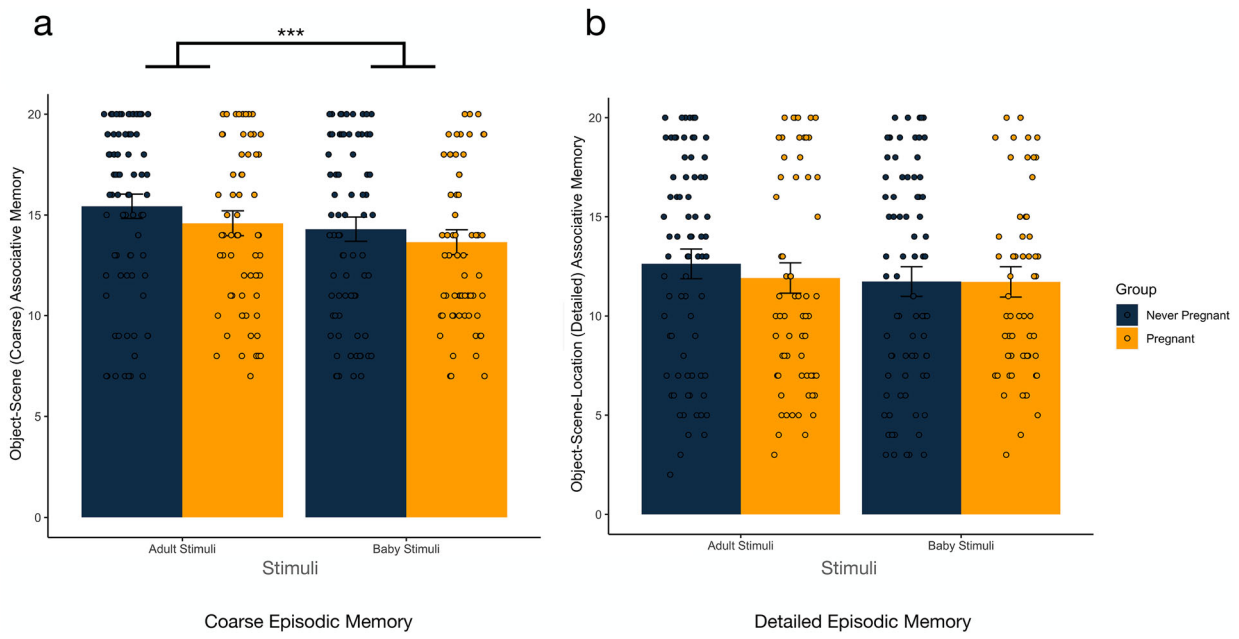


**Figure 3.** Object Recognition Memory at Wave 2. Estimated marginal means from the linear mixed effects models using (a) D-prime, (b) Hit Rate, (c) False Alarm Rate, in pregnant (mustard) and never pregnant (navy) participants at Wave 2 (controlling for Wave 1 performance). Bars indicate the estimated marginal means from the models and the error bars reflect the standard error of those means. Individual participant raw data is plotted overlaid on the bars using dots (jittered along the x-axis for increased visibility of the individual data points). Responses to the adult stimuli from the task are represented in the two leftmost bars for each graph component, and responses to the baby stimuli from the task are represented in the two rightmost bars for each graph. Connecting lines with stars represent the significant contrasts and main effects. * $p < .05$, ** $p < .01$, *** $p < .001$.

baby stimuli at Wave 2, $F(1, 95) = 34.25$, $p < .001$, partial $\eta^2 = .27$ (Figure 4a). There was also an effect of D-prime to adult stimuli at Wave 1, whereby a higher D-prime to adult stimuli at Wave 1 was associated with a higher D-prime overall at Wave 2, $F(1, 87) = 9.96$, $p = .002$, partial $\eta^2 = .10$. No other effects were significant (see supplemental Table S10). For hits, there was an effect of stimuli, whereby hits to adult stimuli were higher than hits to baby stimuli at Wave 2, $F(1, 95) = 19.76$, $p < .001$, partial $\eta^2 = .17$ (Figure 4b). For false alarms there was also an effect of stimuli, whereby false alarms were higher to baby than adult stimuli at Wave 2, $F(1, 95) = 3.96$, $p = .050$, partial $\eta^2 = .04$ (Figure 4c) (see supplemental Table S11-S12 for full results for hits and false alarm models).

### *Control analyses for object-recognition memory*

There was an effect of sleep quality on hits at Wave 2 in the pregnant group, whereby greater sleep quality was associated with a higher hit rate, $F(1, 35) = 11.29$, $p = .002$, partial $\eta^2 = .24$. However, no other associations between sleep quality, parity, or experimental group, on D-prime, hit rate, or false alarm rates at Wave 2 were evident within the pregnant group (see supplemental tables S13a-i). Within the never pregnant group, there was no association between COVID-19 impact score on D-prime, hit rate, or false alarm rates at Wave 2 (see supplemental Table S14a-c). In both groups, there was no association between the time between waves and D-prime, hit rate, or false alarm rates at Wave 2 (see supplemental Table S15a-c).

### *Object-scene associative memory*

For the coarse episodic memory index, there was a significant effect of group, whereby the pregnant group had higher accuracy scores overall (regardless of stimuli) than the never pregnant group, $F(1, 90) = 5.35$, $p = .023$, partial $\eta^2 = .06$, and an effect of stimuli, whereby accuracy for adult stimuli was higher than accuracy for baby stimuli (regardless of group), $F(1, 98) = 51.14$, $p < .001$, partial $\eta^2 = .34$ (Figure 5a). There was also an effect of accuracy for adult stimuli at Wave 1, $F(1, 90) = 14.63$, $p < .001$, partial $\eta^2 = .14$, and baby stimuli at Wave 1, $F(1, 90) = 28.48$, $p < .001$, partial $\eta^2 = .24$, whereby higher accuracy to either stimuli at Wave 1 was associated with higher accuracy overall at Wave 2. No other main effects nor interactions were significant (see supplemental Table S16).

For the detailed episodic memory index, there was an effect of group, whereby the pregnant group had higher accuracy scores overall (regardless of stimuli) than the never pregnant group, $F(1, 90) = 3.96$, $p = .050$, partial $\eta^2 = .04$, and an effect of stimuli, whereby accuracy for adult stimuli was higher than accuracy for baby stimuli (regardless of group), $F(1, 98) = 10.61$, $p = .002$, partial $\eta^2 = .01$ (Figure 5b). There was also an effect of accuracy for adult, $F(1, 90) = 13.59$, $p < .001$, partial $\eta^2 = .13$, and baby stimuli, $F(1, 90) = 17.74$, $p < .001$, partial $\eta^2 = .17$, at Wave 1, whereby higher accuracy to either stimuli at Wave 1 was associated with higher accuracy overall at Wave 2. No other main effects nor interactions were significant (see supplemental Table S17).

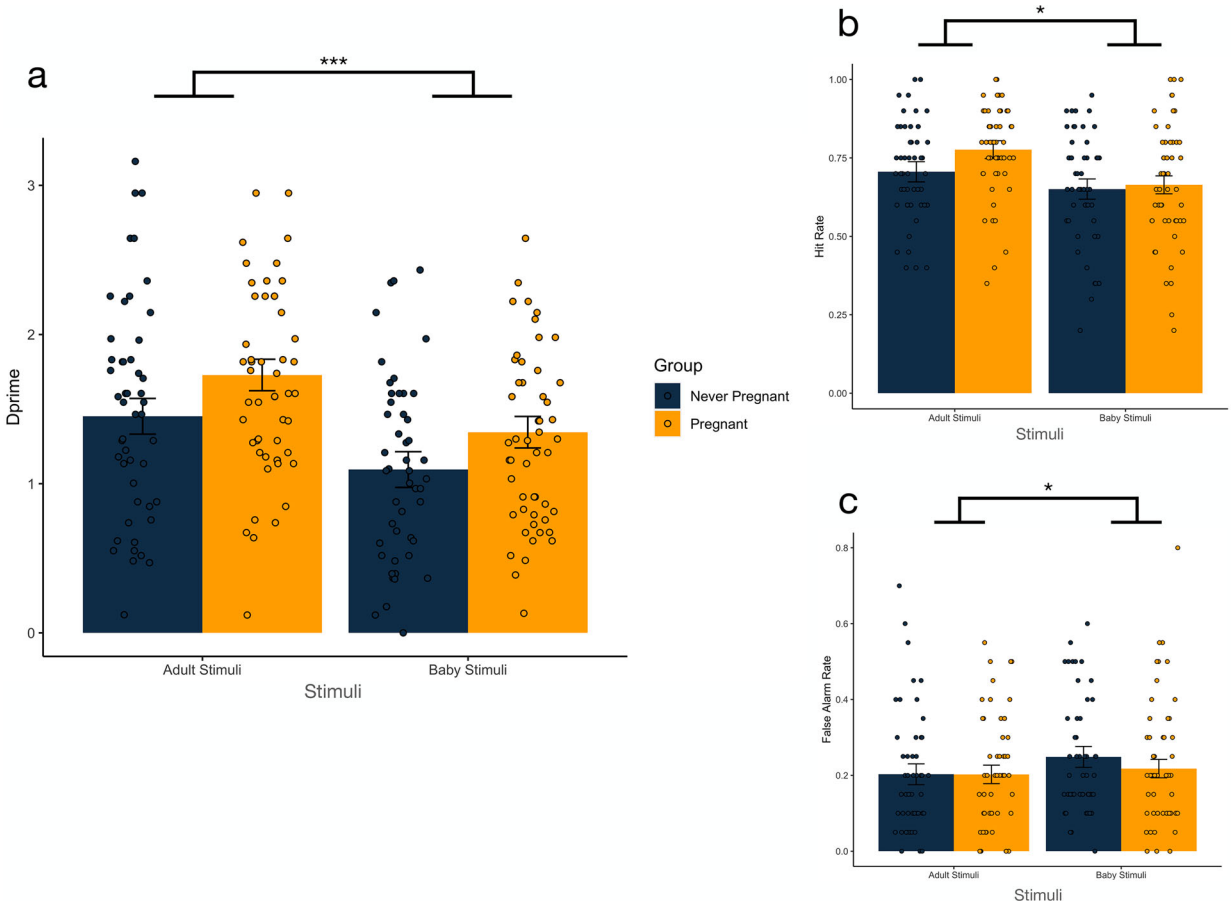


**Figure 4.** Object-Scene Associative Memory at Wave 1. Estimated marginal means from the linear mixed effects models using (a) coarse episodic memory (object-scene associative memory), and (b) detailed episodic memory (object-scene-location associative memory), in pregnant (mustard) and never pregnant (navy) participants at Wave 1. Bars indicate the estimated marginal means from the models and the error bars reflect the standard error of those means. Individual participant raw data is plotted overlaid on the bars using dots (jittered along the x-axis for increased visibility of the individual data points). Responses to the adult stimuli from the task are represented in the two leftmost bars for each graph component, and responses to the baby stimuli from the task are represented in the two rightmost bars for each graph. Connecting lines with stars represent the significant contrasts and main effects. * $p < .05$, ** $p < .01$, *** $p < .001$.

### *Control analyses for object-scene associative memory*

Within the pregnant group, there was no effect of sleep quality, parity, or RCT experimental group on coarse or detailed episodic memory at Wave 2 (see supplemental tables S18a-f). Within the never pregnant group, there was no association between COVID-19 impact score and either coarse or detailed associative memory at Wave 2 (see supplemental Table S19a-b). In both groups, there was no association between the time between waves and coarse or detailed episodic memory at Wave 2 (see supplemental Table S20a-c).

### *Further control analyses*

As an additional robustness check, analyses of D-prime, coarse and detailed associative memory at Wave 1 and Wave 2 were again performed comparing performance in the never pregnant group to that in the pregnant participants who did not receive the relaxation intervention in the RCT (i.e., who were in the RCT control group). This reduced the sample size of the pregnant group from N = 70 to N = 40 for object-recognition memory Wave 1, from N = 51 to N = 36 for object-recognition memory Wave 2, from N = 65 to N = 23 for associative memory Wave 1, and from N = 37 to N = 23 for associative memory Wave 2. As can be seen in tables S21-S26, results for the analyses remained the same except for the effect of stimuli and group which were reduced to trend associations for associative memory Wave 1 and 2, consistent with the reduction in power based on a smaller sample size.

To further check that elevated depression within the never pregnant group was not influencing the results, we reran analyses of D-prime, coarse and detailed associative memory at Wave 1 and Wave 2 excluding the never pregnant group tested in person who had lower average depression scores (7.89) than the never pregnant group tested online (12.46), again controlling for depression levels. Results were identical in those analyses, which are

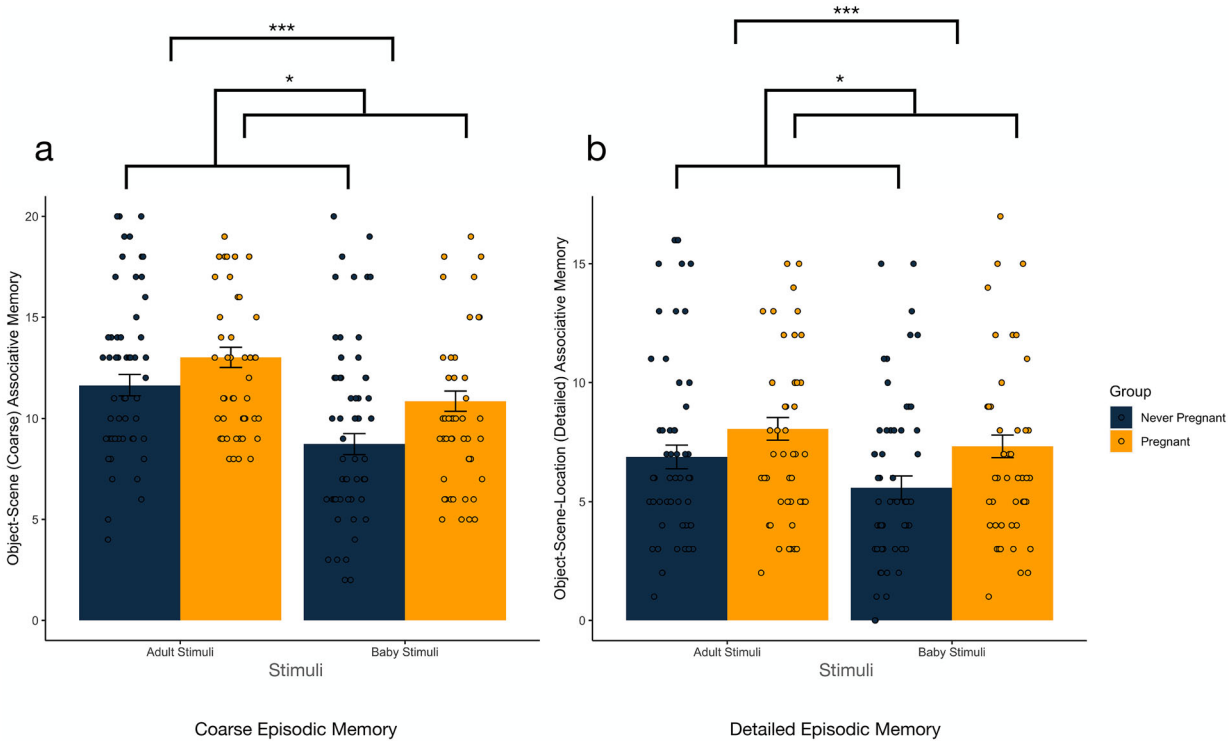


**Figure 5.** Object-Scene Associative Memory at Wave 2. Estimated marginal means from the linear mixed effects models using (a) coarse episodic memory (object-scene associative memory), and (b) detailed episodic memory (object-scene-location associative memory), in pregnant (mustard) and never pregnant (navy) participants at Wave 1. Bars indicate the estimated marginal means from the models and the error bars reflect the standard error of those means. Individual participant raw data is plotted overlaid on the bars using dots (jittered along the x-axis for increased visibility of the individual data points). Responses to the adult stimuli from the task are represented in the two leftmost bars for each graph component, and responses to the baby stimuli from the task are represented in the two rightmost bars for each graph. Connecting lines with stars represent the significant contrasts and main effects. * $p < .05$, ** $p < .01$, *** $p < .001$.

presented in tables S27-S32. Notably, in none of those analyses was depression score a significant predictor of performance.

## Discussion

Here we set out to test whether pregnant women showed either attentional orienting towards baby stimuli (perhaps at the expense of adult stimuli) and/or a general enhancement in memory on a task that is highly dependent on hippocampal function (spatial associative memory). We saw evidence for attentional orienting and general cognitive enhancement effects. First, in the immediate memory test, for the less hippocampally-mediated task (object recognition memory), we observed that pregnant women, but not never pregnant women, showed an initial boost in learning about objects that were related to pregnancy and motherhood (higher performance accuracy for baby objects relative to adult objects in the immediate test), and performed marginally better than the never pregnant women for learning about baby items. However, this boost in learning did not transfer to enhanced long-term memory for those specific objects, with both pregnant and never pregnant women showing comparable object-recognition memory to adult and baby items at the 4-week delayed test. Second, despite pregnant and never pregnant women exhibiting similar performance on both the coarse and detailed memory metrics from the object-scene associative memory test performed immediately after learning, pregnant women exhibited higher performance accuracy than never pregnant women on those same tests 4-weeks after learning. Importantly, this task was designed to mimic the hippocampal-dependent nature of prior cognitive tasks in rodents where performance has been shown to be enhanced during pregnancy (Kinsley et al., 2014; Lambert et al., 2005; Love et al., 2005; Macbeth et al., 2008a, 2008b; Paris & Frye, 2008; Pawluski et al., 2006), suggesting that the long term retention of hippocampal-based memories is generally enhanced during pregnancy. Taken together, these data show that the behavioural plasticity of pregnancy was expressed in different ways according to the type of memory assessed (associative vs. object memory), the timing of assessment (immediate or 4 weeks after learning), and the ecological relevance of the stimuli used (relevant to pregnancy and motherhood or not; see Table 4 for a summary).

The primary finding of this study, that pregnancy in humans was associated with enhanced long-term associative memory performance, is largely consistent with reports in the non-human animal literature on pregnancy-associated cognitive improvements, particularly on spatial and associative tasks that are hippocampal dependent

(Kinsley et al., 2014; Lambert et al., 2005; Love et al., 2005; Macbeth et al., 2008a, 2008b; Paris & Frye, 2008; Pawluski et al., 2006). Notably, hormones involved in pregnancy have been shown to affect hippocampal long-term potentiation (LTP), and modulate fast spiking interneurons in the hippocampus (Owen et al., 2013), both of which are critical physiological functions involved in learning and memory. Although we did not assess hippocampal contributions to enhanced long-term associative memory performance in the current study, we have previously reported using fMRI in children that delay (~2 weeks after learning) performance on a variant of the task used here is associated with multivariate stabilisation signatures in the hippocampus (Callaghan et al., 2021). Interestingly, in this study, pregnancy was only associated with enhancements in long-term associative memory, not associative learning, hinting that the previously reported multivariate memory stabilisation signatures in the hippocampus may be augmented during pregnancy, which could be tested in future studies. Hence, in line with our hypotheses, it is possible that general enhancements in cognitive functioning during pregnancy may be specific to tasks that heavily tax the hippocampus.

Understanding how specific neural circuits are affected by the experience of pregnancy may also help to elucidate why some past studies have reported either no change or decrements in cognitive performance among pregnant, relative to never-pregnant women (Christensen et al., 2010; Glynn, 2012; Henry & Rendell, 2007). In prior work, impairments in cognitive functioning during pregnancy appear to be restricted to verbal paired associates (VPA) tasks, and tasks which rely on free recall (Christensen et al., 2010; Glynn, 2012; Henry & Rendell, 2007). While VPA is an associative task and does activate the hippocampus, studies have shown that the extent of hippocampal engagement during VPA may be associated with scene imagery, rather than the binding nature of the associative task, *per se* (Clark et al., 2018). Similarly, hippocampal engagement during free recall tasks is also content-dependent, with higher hippocampal engagement required in the recall of scenes relative to objects (Ross et al., 2019). In the current study, we utilised a visual associative task that relied on object-scene associations, and which would therefore be expected to more heavily depend on the hippocampus than past studies using VPA. As such, future studies examining neural mechanisms underlying cognitive change in pregnancy should not only assess the object-scene associative memory task used here, but should contrast performance on that task with performance on free recall or VPA tasks, in which pregnant women are known to be impaired. Such comparisons will help to reveal the specific task conditions (e.g., spatial information, verbal vs. visual memory) and neural circuits (e.g., hippocampal or cortical) under which pregnancy-associated cognitive enhancements vs. decrements are observed.

While consideration of neural networks may help to explain general performance boosts seen in pregnant women on the object-scene associative test, this neural perspective cannot account for the immediate memory boost (in hits and sensitivity) of pregnant women to ecologically-relevant (baby stimuli) objects. Instead, expertise and attentional factors may better explain why pregnant participants exhibited learning enhancements for baby objects specifically. Indeed, expertise and domain knowledge have been consistently shown to enhance memory for domain-relevant visual and motoric information, such as chess positions (Bilalić et al., 2009), dance steps (Allard & Starkes, 1991), and maps (Gilhooly et al., 1988). Importantly, this enhanced memory for domain-relevant information does not come at the expense of general memory, with experts performing at similar levels as non-experts for information which falls outside their area of expertise (Evans et al., 2011). In the current study, pregnant women in the third trimester of pregnancy might be considered as having gained expertise with the objects within the pregnancy category due to enhanced experience with those objects, which could explain their short-term boost in performance for that category. In contrast, both pregnant and never pregnant women would likely have similar levels of expertise as one another in the category of adult objects, and their performance did not differ from one another for that category. However, if the expertise explanation was sufficient, we might also predict an effect of parity, with sensitivity and hits for baby objects increasing with each successive pregnancy, which was not observed in this study. Given the necessary length of time between successive pregnancies (9 + months), it is possible that expertise is lost and rebuilt with each successive pregnancy. Alternatively, it may also be true that pregnancy brings with it an enhanced attentional state towards ecologically relevant items, and that attentional state interacts with expertise to bring about domain-specific improvements in immediate object-recognition memory. Both of these alternatives will have to be tested in future studies.

Considering the potential expertise effects observed here for object recognition learning, it is interesting to consider what the benefit of a domain-general enhancement in long-term visual spatial associative memory in pregnancy might be. One past example in the human fMRI literature may be informative (Parsons et al., 2017). In that study, mothers showed greater reactivity than non-mothers to vocalisations from both adults and infants in a range of cortical regions implicated in auditory affective processing (e.g., the amygdala). However, mothers with older infants (up to 14 months of age) showed increasing activity in these cortical regions for the infant relative to the adult sounds, suggesting that maternal experience could build upon an initially general enhancement in affective vocal processing. It will be important for future studies to track pregnant women into the postpartum period to establish whether the

general enhancement in long-term visual spatial associative memory observed here to both adult and baby stimuli becomes stronger to baby stimuli further along in the postpartum months.

One additional factor worth considering in the interpretation of the cognitive enhancements seen during pregnancy in the current study is that the sample of pregnant participants assessed here was not confounded by mood disorders. In the current sample, the pregnant participants actually had lower depression scores than the control group of never pregnant women, which was likely a product of the never pregnant group being collected during a global pandemic when rates of mood disorders in the adult population have increased (Twenge & Joiner, 2020). In humans, cognitive deficits in pregnancy have recently been shown to be specific to women who had elevated anxiety and depressive symptoms (Kataja et al., 2017; Ouellette & Hampson, 2019). In rats, pregnancy associated enhancements in hippocampally-mediated spatial memory across the lifespan were not observed in animals who were exposed to a gestational stressor (Lemaire et al., 2006), which might approximate mood disturbance in humans. Although we controlled for depressive symptoms, and depressive symptoms were rarely associated with memory performance, it will be important to explore how mood in pregnancy interacts with the brain, attention, and expertise to affect memory performance on the task used here.

In conclusion, the data from this study clearly demonstrate that rather than exhibiting vast impairments in memory during the perinatal period, women in the third trimester of pregnancy show general enhancements in long-term visual spatial associative memory, and a short-term boost in object-recognition memory for ecologically relevant stimuli. Whether these enhancements persist and evolve into the postpartum period, and their functional significance for the role of motherhood remain open questions for future research.

## Limitations

The data contained in this manuscript should be interpreted in light of several study limitations. Possibly the largest limitation is that the control group of never pregnant women were collected between September – October 2020 during the global pandemic of COVID-19, and were also experiencing higher levels of depression symptoms than the pregnant group (likely because of the effect of the pandemic on mental health). As depression is known to affect hippocampal-dependent memory (Barch et al., 2019; Hickie et al., 2005), it is possible that the never pregnant group may have performed better on the immediate associative task had their depression levels been lower. Nonetheless, as we only observed differences between the groups on the delay memory test, our results indicate that even when learning levels were matched, pregnant women performed better than never pregnant women in the retention of that information over time. We also took several steps to control for potential influences of depression in our study, including using depression as a covariate. These control analyses revealed that depression symptoms were rarely associated with either object-recognition memory or object-scene associative memory. In addition, we reran the analyses excluding the never pregnant group collected in person. As that group had relatively lower levels of depression than the never pregnant group collected online, by excluding them we would enhance our chance of detecting an effect of depression if one existed. The results were identical. Finally, we controlled for the psychological impact of the pandemic beyond depressive symptoms by including participant's rating of the global impact COVID-19 was having on their lives within the never pregnant group tested online. COVID-19 impact scores were never associated with object-recognition memory or object-scene associative memory. As such, we are confident that depression differences between groups, and any diffuse psychological impact of COVID-19, were not significant influential factors in this study.

Another limitation of this study is that the data for the never pregnant group were largely collected online, while the data from pregnant women were collected in-person, which also resulted in a more geographically homogenous sample for the pregnancy group (collected from New York City) than for the never pregnant group (collected from within the United States; information on geographic region within the United States was not collected). We took several steps to address these group differences. Given the higher likelihood for participant inattention online, we performed strict data exclusions for participants who were performing below chance levels, as well as included an attention check during training (on which performance was universally high, though it was a simple attention check task). Together, the attention check during training, the exclusions of low performers at test, and the fact that the results followed an expected pattern (high hits, low false alarms, better performance on coarse than detailed associative memory task) increase the confidence in our results. With those checks in place, the data were clear in showing that the performance of the pregnant and never pregnant participants was matched at Wave 1 for adult items in the object-recognition test, and for both adult and baby associations in the object-scene association tests. Although information on geographic region was limited to the pregnant group, we did collect information from all participants on factors that might relate to geography and which could feasibly be associated with memory performance, including ethnicity, race, education, and income. These variables were used as covariates in the analyses and were never associated with the memory measures. As such, we are confident that the collection of data in the never pregnant group during the COVID-19 pandemic

did not grossly affect their performance on the memory tasks.

Another limitation in the current study is that the data from the pregnant women were collected as part of a larger study involving a randomised control trial (RCT) of a relaxation intervention. We had no expectation that women's group assignment in the RCT would influence their performance on the memory task assessed here, and we also confirmed the validity of that assumption by performing additional analyses within the pregnancy group demonstrating no such associations existed, including rerunning analyses with the pregnant participants who received the active relaxation treatment excluded. Nonetheless, future studies in community samples of pregnant women will be required to strengthen confidence in the results reported here.

Beyond these study limitations, there were also many strong features of the study design, including a relatively large sample size for a difficult to study population, good retention of study participants across time (23-25% attrition), and a control sample of never pregnant (i.e., nulliparous), rather than not-pregnant but parous mothers. Moreover, we examined a novel task in this population, revealing an interesting set of results on which future studies can build. We recommend that future research investigate ecologically relevant stimuli, and engage tasks that go beyond the standard cognitive battery used in past work and tax different neural systems, to determine the nuanced effects of pregnancy on cognition and fully characterise the brain plasticity behind the transition to parenthood.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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