Effects of Parenthood on Neural Responses to Pup-Related Cues

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ABSTRACT

The onset of parental care in female mammals is associated with plasticity in neural processing of infant-related sensory stimuli, which enhances mothers' ability to detect and care for their offspring; however, little is known about sensory plasticity in fathers. We tested the hypothesis that parenthood alters neural responses to olfactory and auditory stimuli from infants in male and female California mice (*Peromyscus californicus*), a biparental rodent. Virgins and new parents of both sexes were exposed to a combination of a chemosensory stimulus (pup-scented or unscented cotton [control]) and an auditory stimulus (pup vocalizations or white noise [control]). Brains were collected one hour later and stained immunohistochemically for Fos, an index of neural activity. We quantified Fos in the main olfactory bulbs (MOB), a region essential to receiving olfactory information, and medial preoptic area (MPOA), a region critical for parental behavior. We predicted that Fos in MOB and MPOA would be greater in parents than virgins, especially after exposure to pup stimuli. We found that in females, MPOA and MOB Fos did not differ between virgins and mothers or across treatment groups. In contrast, fathers had lower expression of Fos in MOB but higher expression in MPOA, compared to virgin males. Moreover, Fos in MPOA was higher in males exposed to pup vocalizations and pup scent compared to those exposed exclusively to pup vocalizations. Fos in MPOA was also higher in males exposed to scent or both scent and vocalization stimuli compared to males exposed to control stimuli. These findings suggest that the onset of parenthood alters activity in the MOB and MPOA, especially in response to pup vocalizations and scents, in males but not females in this biparental rodent.

KEYWORDS: audition, biparental care, brain, California mouse, neural plasticity, olfaction, parental behavior

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INTRODUCTION

Maternal care, or the care of young by their mother, is essential for offspring survival in all mammalian species. The onset of maternal care is associated with neural plasticity in the mother's brain, mediated by hormonal changes that mothers experience during pregnancy, parturition and lactation (Horrell et al., 2021). Neural plasticity refers to the reorganization of neural pathways in the brain and can include changes in the production, survival, morphology, and activity of neurons and synapses. These structural and functional changes in the brains of new mothers can enable mothers to behave appropriately toward their offspring.

Paternal care – i.e., the care of offspring by fathers – is also important for offspring survival and development in some mammals, including humans; however, relatively little is known about the neural mechanisms underlying the onset of paternal behavior. California mice (*Peromyscus californicus*) are one of the few mammals that are biparental, meaning that both parents provide care for their offspring (Gubernick et al., 1987); thus, they are a useful model for examining the neural mechanisms underlying the onset of parental care in both sexes. Both mothers and fathers in this species are strongly attracted to their offspring and begin to huddle, lick, and carry pups shortly after parturition. Parents are also strongly attracted to and nurturant toward unrelated pups (de Jong et al., 2009; Perea-Rodriguez et al., 2015; Horrell et al., 2017; Perea-Rodriguez et al., 2018). In contrast, virgin adult males and females often avoid or attack experimentally presented pups (Gubernick et al., 1994; de Jong et al., 2009; Horrell et al., 2017; Nguyen et al., 2020).

One type of neural plasticity associated with the onset of offspring care by mothers is sensory plasticity, which refers to neural changes in pathways involved in detecting and processing sensory stimuli. For example, in CBA/CaJ house mice (*Mus musculus*), new mothers undergo changes in the brain's auditory pathway that enhance their ability to detect pup vocalizations (Dunlap et al., 2020). In addition, during the onset of motherhood, some mammals, including house mice, have a significant increase in neurogenesis (i.e., production of new neurons) in the olfactory bulbs, the first brain regions that receive information about olfactory stimuli (Medina & Workman, 2020). Some evidence suggests that fathers, too, undergo plasticity in sensory systems. For example, increased neurogenesis in the olfactory bulb has been found in C57BL6 house mouse fathers (Mak & Weiss, 2010), similar to mothers. However, sensory plasticity in fathers has received very little attention, especially in biparental species. Characterizing this plasticity in fathers and elucidating the underlying neural and neuroendocrine mechanisms would enhance our understanding of both the effects of fatherhood on the brain and, conversely, the neural processes underlying the onset of paternal care.

This study investigated the neural pathways that are activated in response to pup-related sensory stimuli – pup scents and vocalizations – in male and female California mice, as well as the effects of parenthood on these neural responses. Neural pathways involved in olfactory and auditory processing interact with pathways involved in the onset of parental care, suggesting that olfaction and audition may be important sensory modalities for parental care, at least in rodents (Kuroda et al., 2011; Horrell et al., 2019; Wilson et al., 2022). The main olfactory bulbs (MOB) are essential for the detection of chemosensory stimuli and may have downstream effects on parental behavior by sending information to other brain regions. One such region is the medial preoptic area (MPOA), which is crucial for parental behavior in both males and females (Numan et al., 2005; Akther et al., 2014; Bales & Saltzman, 2016; Horrell et al., 2019). The MPOA also receives information from the auditory system, suggesting

that sounds, in addition to scents, can influence parental care. Therefore, we tested the hypotheses that the MOB and MPOA of male and female California mice have greater neural responses to pup sensory stimuli compared to control stimuli, that parents have greater neural responses to pup sensory stimuli compared to virgins, and that new parents exposed simultaneously to auditory and olfactory stimuli have greater neural responses compared to those exposed to an isolated stimulus.

METHODS

Animals

Subjects were descended from California mice purchased from the Peromyscus Genetic Stock Center (University of South Carolina, Columbia, SC, USA) and were bred at the University of California, Riverside (UCR). Mice were housed in polycarbonate cages (44 × 24 × 20 cm) under standard laboratory conditions (Nguyen et al., 2020). At weaning age (27–31 days), before the birth of younger siblings, animals were removed from their parents' cages and housed in groups of 3-4 same-sex, age-matched mice until used in the study.

We used 32 breeding pairs housed with their first litter of pups and 29 virgin pairs consisting of a reproductively inexperienced male and an ovariectomized female. Ovariectomies (i.e., surgical removal of both ovaries) were performed as previously described (Zhao et al., 2018; Andrew et al., 2019), 10 days prior to pair formation. Breeding females underwent sham-ovariectomies at the same time point to control for non-specific effects of surgery.

Stimulus Exposure

Each adult mouse underwent a single stimulus-exposure test (**Table 1**). The subject was placed alone in a clean cage for 110 minutes to allow it to acclimate to the cage. An auditory stimulus and a chemosensory stimulus were then introduced for 10 minutes. The auditory stimulus consisted of either pre-recorded vocalizations from an unrelated pup or white noise (control), and the chemosensory stimulus was either cotton containing the scent of an unrelated pup or fresh cotton (control); the cotton was contained in a wire mesh tea ball (Ø: 8 cm) to prevent the mouse from handling it. To obtain the pup scent, an unrelated 3- to 7-day old pup was wiped with a cotton ball 30 times across its ventrum and anogenital region. Tests were conducted in a sound-attenuated room at 08:00-09:00 h. We performed tests during lights-on, which is the inactive period for nocturnal animals, to reduce the amount of background neural activity. Parents were tested 4-6 days after the birth of their first litter, and virgins were tested at a comparable age and time point. Male and female pair mates were tested on the same day, with the female's test beginning 20 minutes after the beginning of her mate's test.

Pup Stimulus	Stimulus Pair	Male Sample Size	Female Sample Size
Pup Scent	White noise + **Pup cotton**	8 fathers, 8 virgin males	8 mothers, 6 virgin females
Pup Call	**Pup calls** + Fresh cotton	8 fathers, 6 virgin males	8 mothers, 8 virgin females
Pup Call + Pup Scent	**Pup calls** + **Pup cotton**	8 fathers, 8 virgin males	8 mothers, 8 virgin females
Control	White noise + Fresh cotton	8 fathers, 7 virgin males	8 mothers, 8 virgin females

Table 1: Experimental design

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Brain Collection and Immunohistochemistry

To determine neural responses to stimuli, we quantified expression of Fos, the protein product of the immediate early gene c-fos, in the MOB and MPOA of male and female subjects. c-fos and other immediate early genes are expressed in neurons during genomic activation, beginning approximately 1 hour after exposure to a stimulus, and their protein products can be used as indicators of neural activity (Kovács, 2008).

One hour after the end of stimulus exposure, mice were deeply anesthetized with pentobarbital and euthanized via transcardial perfusion with cold phosphate-buffered saline (PBS 0.1M) and paraformaldehyde (PFA) (de Jong et al., 2009). Brains were harvested and stored for 48 hours in 4% PFA at 4°C. The tissue was then moved to a 30% sucrose solution until fully saturated, then cryoprotected and stored at -20°C.

Brains were sliced into 40 µm-thick coronal sections using a cryostat. Sections were stained immunohistochemically for Fos using Anti-rabbit c-Fos antibody followed by Alexfluor 555 as the second antibody, allowing for visualization of Fos-positive cells as green in color. Stained tissues were mounted onto slides and imaged with a Zeiss 880 inverted confocal microscope. Lastly, a researcher blind to the stimulus treatment quantified Fos-positive cells using QuPath software (Bankhead et al., 2017). Fos-positive cells were counted in a square section with an area of 200 x 200 μm^2 within the MOB and MPOA.

Statistical Analysis

Fos data were square-root transformed and analyzed by linear mixed-effect models. The model for each brain region included reproductive status, stimulus treatment, and their interaction. Data from males and females were analyzed separately. Significant effects and interactions were further investigated using pairwise post-hoc comparisons. We did not compare the sexes directly because male and female brains were processed, stained, and imaged in different time periods, which might have affected Fos expression.

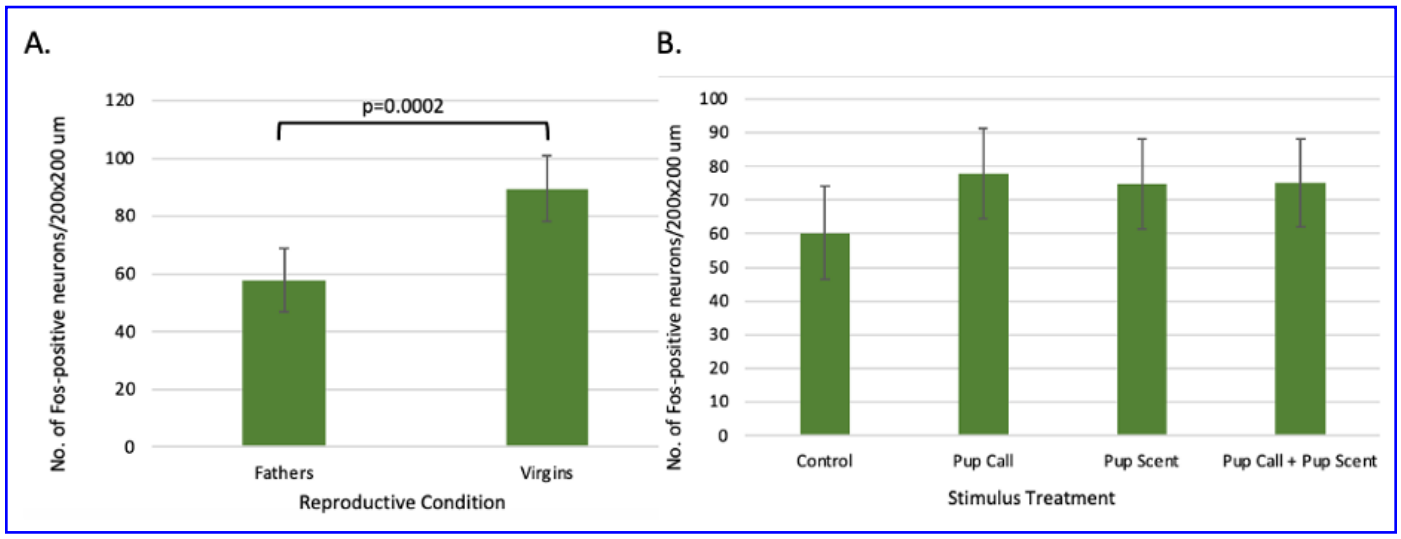

Figure 1: Number of Fos-positive cells (mean ± SE, non-transformed) in the MOB of male California mice. A: Comparison of fathers (N = 30) and virgin males (N = 29) collapsed across the four stimulus treatments. B: Comparison across stimulus treatments for fathers and virgins combined (N = 14 Control, 14 Pup Call, 14 Pup Scent, 17 Pup Scent + Pup Call; P = 0.768).

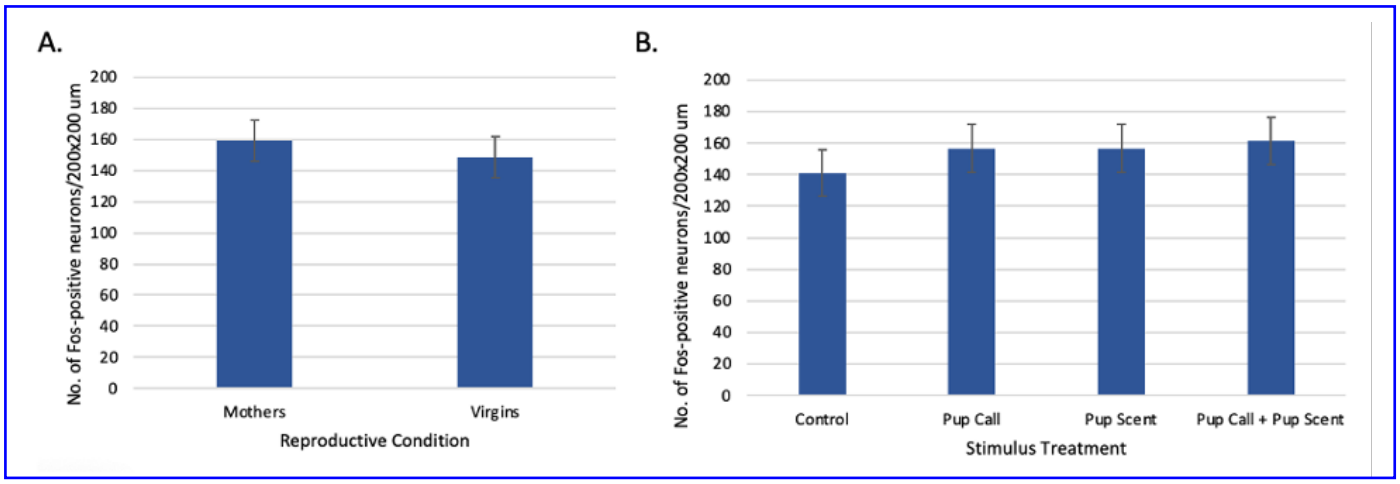

Figure 2: Number of Fos-positive cells (mean ± SE, non-transformed) in the MOB of female California mice. A: Comparison of mothers (N = 32) and virgin females (N = 30) collapsed across the four stimulus treatments (P = 0.433).B: Comparison across stimulus treatments for mothers and virgin females combined (N = 15 Control, 15 Pup Call, 11 Pup Scent, 12 Pup Scent + Pup Call; P = 0.431).

RESULTS

Main Olfactory Bulbs

In male mice, Fos expression in the MOB was significantly higher in virgins than in fathers ($\chi 2 = 13.44$, $P = 0.0002$), but no significant difference was found among stimulus treatments ($\chi 2 = 1.14$, $P = 0.768$) (**Fig. 1**). In females, MOB Fos expression did not differ significantly between virgins and mothers ($\chi 2 = 0.61$, $P = 0.433$) or among stimulus treatments ($\chi 2 = 2.75$, $P = 0.431$) (**Fig. 2**).

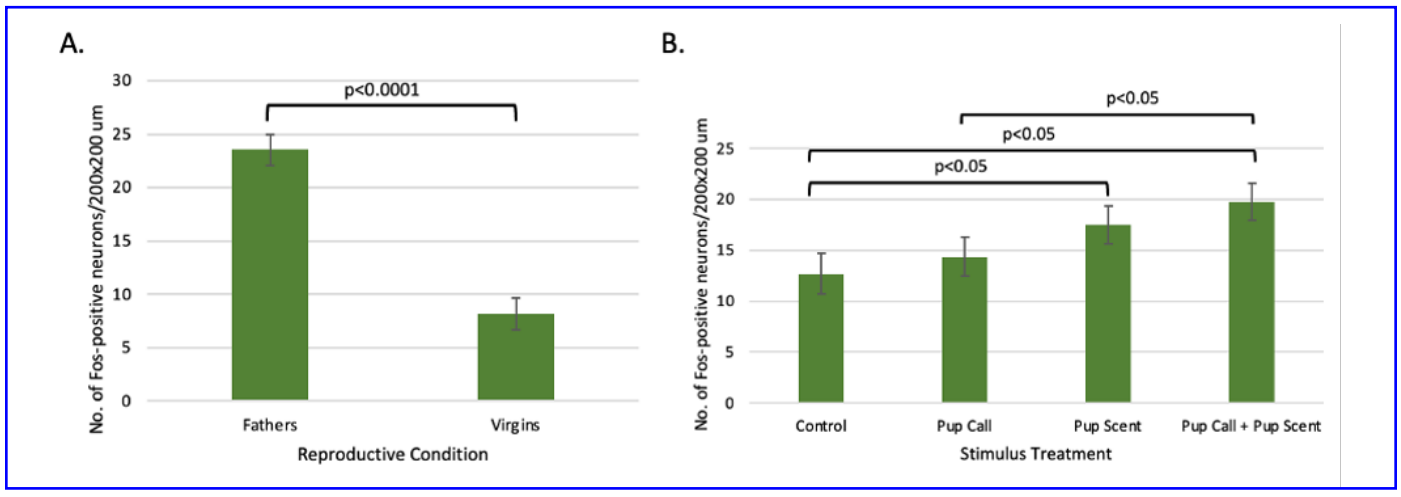

Figure 3: Number of Fos-positive cells (mean ± SE, non-transformed) in the MPOA of male California mice. A: Comparison of fathers (N = 32) and virgin males (N = 29) collapsed across the four stimulus treatments. B: Comparison across stimulus treatments for fathers and virgins combined (N = 15 Control, 14 Pup Call, 16 Pup Scent, 16 Pup Scent + Pup Call; P = 0.010).

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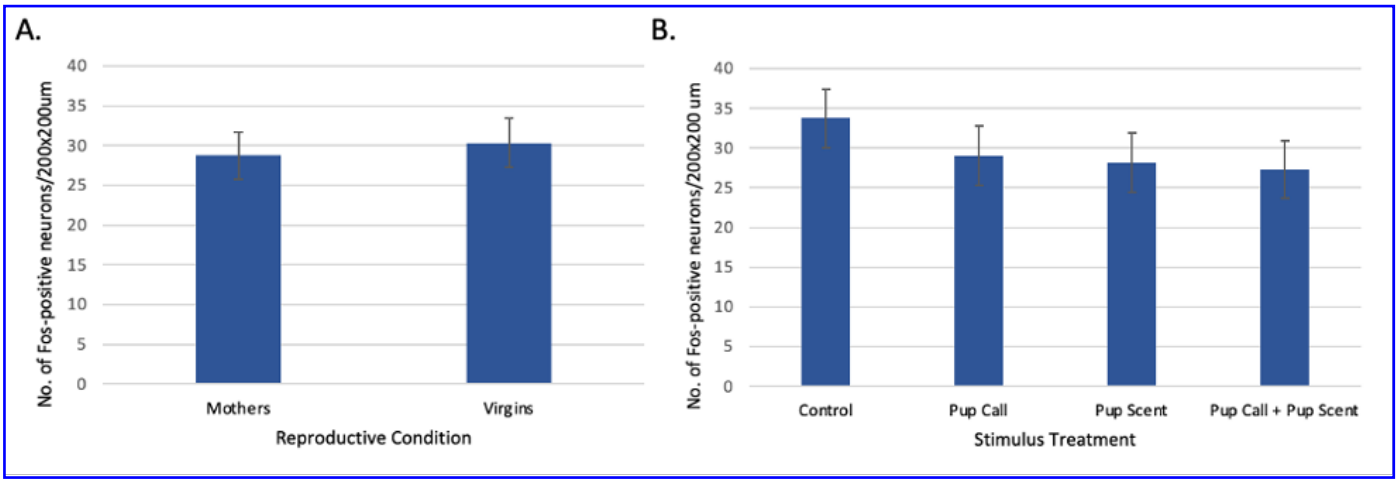

Figure 4: Number of Fos-positive cells (mean ± SE, non-transformed) in the MPOA of female California mice. A: Comparison of mothers (N = 28) and virgin females (N = 25) collapsed across the four stimulus treatments (P = 0.433).B: Comparison across stimulus treatments for mothers and virgin females combined (N = 15 Control, 15 Pup Call, 11 Pup Scent, 12 Pup Scent + Pup Call; P = 0.801).

Medial Preoptic Area

In males, Fos expression in the MPOA was significantly higher in fathers than in virgins ($\chi 2 = 108.70$, $P<0.0001$). Moreover, for fathers and virgin males combined, MPOA Fos differed significantly among treatments ($\chi 2 = 11.32$, $P = 0.010$). Fos expression in the MPOA was significantly higher in males exposed to pup scent only or to both pup calls and pup scent, as compared to males exposed to the control stimuli (P's < 0.05). Additionally, Fos expression was higher in males exposed to both stimuli than in those exposed only to pup calls (**Fig. 3**). In females, Fos expression in the MPOA did not differ significantly between mothers and virgins ($\chi 2 = 1.88$, $P = 0.598$) or among stimulus treatments ($\chi 2 = 0.06$, $P= 0.801$) (**Fig. 4**).

DISCUSSION

The mechanisms underlying the onset of male parental care in biparental mammals are not well understood. Specifically, little is known about the role of sensory plasticity in the onset of paternal behavior. In this study, we show that in male California mice, Fos expression was influenced by both reproductive status (MOB and MPOA) and stimulus treatment (MPOA only), whereas neither of these factors affected Fos expression in the MOB or MPOA in females.

Males

In contrast to our prediction, neural activity in the MOB was lower in fathers than in virgin males but did not differ among stimulus treatments for fathers and virgins combined. Previous studies have investigated the role of MOB in infant-directed behaviors and neurogenesis in male rodents. Kirkpatrick et al. (1994) found that in the biparental prairie vole (*Microtus ochrogaster*), males that underwent olfactory bulbectomy or lesions of the MOB attacked pups more frequently than did control males, suggesting that the MOB is important for inhibiting aggression towards pups. Mak & Weiss (2010) investigated neural plasticity in house mouse fathers and found that neurogenesis in MOB plays a role in offspring recognition. Although these studies implicate the MOB in the expression of pup-directed behavior, we know of no published studies investigating neural responses to pup stimuli in the MOB of males.

In the MPOA, as predicted, Fos expression was higher in fathers than in virgin males. This finding aligns with a previous study in our lab that found higher Fos expression in MPOA of California mouse fathers compared to virgins when males were exposed to a pup (de Jong et al., 2009; Horrell et al., 2017). Lambert et al. (2013) also found that in both the California mouse and the uniparental deer mouse (*Peromyscus maniculatus*), fathers exposed to a pup in distress had higher Fos expression in MPOA than virgin males. Because fathers in our study had higher MPOA Fos expression than virgin males in all stimulus treatments, including the control treatment, our results suggest that activity in MPOA, a region critical for parental behavior in both sexes, is altered by fatherhood and that this effect is not dependent on acute exposure to pup stimuli.

For fathers and virgin males combined, Fos expression in MPOA differed among stimulus treatments. Males exposed to pup scent or pup calls and pup scent combined had higher activation than males exposed to control stimuli, while males exposed to pup calls and pup scent combined had higher Fos than those exposed only to pup calls. These findings suggest that a combination of both olfactory and auditory stimuli results in additive or synergistic effects on neuronal activation in MPOA. Similar results have been found in MPOA of house mouse mothers: mothers had higher neural activity when exposed to both pup vocalizations and scents compared to mothers exposed to pup vocalizations or pup scents alone, suggesting that auditory and olfactory stimuli have synergistic effects (Okabe et al., 2013).

Females

In female California mice, Fos expression did not differ between mothers and virgins or across treatments in either the MOB or MPOA. The onset of parenthood in female house mice is associated with an increase in olfactory bulb neurogenesis (Medina & Workman, 2020). The effect of neurogenesis in the olfactory system on parental behavior seems to differ between house mouse fathers and mothers. Although Mak and Weiss (2010) found that neurogenesis in the MOB is important for offspring recognition in fathers, Feierstein et al. (2010) found that disrupted olfactory bulb neurogenesis via focal irradiation of the subventricular zone had no effect on maternal behaviors such as pup retrieval or offspring discrimination abilities in mothers. Our findings on neural responses in California mice, in conjunction with the previous findings on the function of MOB in house mice, suggest that the MOB might play a more important role in parental care in fathers than in mothers.

As previously described, Okabe et al. (2013) found that pup vocalizations and scents had a synergistic effect on neural activity in the MPOA of house mouse mothers. In contrast, the current study found no difference in neural activity in females exposed to one stimulus or both pup calls and pup scent. The discrepancy in findings could potentially be due to differences between the species studied. Moreover, Okabe et al. (2013) investigated new mothers while we studied new mothers and virgin females. Virgin females may not experience the synergistic effect described.

CONCLUSIONS

In summary, we found that the onset of fatherhood alters activity of the MOB and MPOA and that pup chemosensory and auditory stimuli, especially when presented simultaneously, alter activation in MPOA. In contrast, we found that neural activity in the MOB and MPOA was not influenced by reproductive status or stimulus treatment in females.

Our study might have benefited from a larger sample size in order to increase statistical power. Moreover,

performing immunohistochemistry on male and female brains in the same time period would have allowed us to directly compare Fos expression in males and females. Nonetheless, our findings provide novel insight into plasticity in neural responses to pup sensory stimuli during the onset of parenthood and, potentially, into the neural and sensory mechanisms underlying paternal care. Further research investigating responsiveness of other brain regions implicated in receiving and processing of sensory information and parental behavior in response to pup sensory stimuli would contribute to our understanding of male parenting. Moreover, future studies on responsiveness of MOB and MPOA to repeated exposure to pup sensory stimuli, as well as on the cellular and molecular mechanisms of sensory plasticity would provide valuable insight into potential mechanisms underlying the onset of parental care and role of the MOB and MPOA in biparental rodents.

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