

The parental brain: Anatomization of 75 years of neuroscience 1951–2024

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ABSTRACT

Studies of the parental brain have garnered significant attention, revealing neurobiological and psychological changes associated with caregiving. Here, we provide a comprehensive, data-driven overview of the scientific literature on the parental brain, analyzing a large dataset to map the field's knowledge structure. Our objectives include identifying influential authors, contributing countries, publication sources, and commonly used keywords as well as highlighting the most impactful documents and primary thematic areas of research. We analyzed 656 documents (and their 39,302 cited references) from Scopus using CiteSpace software for document co-citation analysis. Our analysis identified 17 key documents, of which the most influential focused on neural correlates of maternal and romantic love and maternal brain responses to infant cues in relation to attachment style. Our analysis additionally identified 10 major thematic domains in the parental brain literature. Qualitative analysis of research clusters revealed a trajectory in the study of the parental brain, progressing from foundational studies on dendritic spine density and maternal memory to the exploration of shared mammalian and human-specific brain networks underlying parental behaviors. Our study points to a growing interest in understanding neurobiological changes in fathers, with parental involvement and exposure to infant cues as moderating factors. The parental brain is a plastic, dynamic network, with bio-behavioral synchrony playing a central role as an interpersonal mechanism that enhances specificity of attachments.

1. Introduction

The neurobiology of parental behavior emerged as a major focus in scientific research from Lorenz (1935)'s foundational studies of social bonds and Bowlby (1969)'s formulation of attachment theory. Decades of studies since have revealed that, across mammalian species, the transition to parenthood profoundly reshapes neurobiological systems and behaviors (Pawluski, 2024). The peripartum period is marked by heightened neuroplasticity (Kim et al., 2010a), structural and functional modifications in the amygdala and reward circuits (Swain et al., 2014), and intensification of oxytocin in subcortical networks (Strathearn et al., 2009). In humans, these adaptations together underpin socio-cognitive processes especially pertinent to parenting, such as sensitive, responsive, and empathic care of offspring (Leuner and Sabihi, 2016; Pawluski et al., 2016; Slattery and Hiller, 2016; Sokolowski and Corbin, 2012). Collectively, these neurobiological changes give evidence of an evolutionary strategy finely tuned to enhance offspring survival and fitness by aligning parental neurobiology with the needs of progeny (Feldman,

2015).

The neurobiological adaptations associated with parenthood are largely conserved across mammalian species, but notable variations arise in response to differing ecological pressures, social structures, and caregiving strategies. For instance, in rodents, parental relationships are typically non-exclusive and transient (Feldman, 2017). In contrast, primates and humans exhibit adaptations that support prolonged caregiving and complex social interactions (Feldman, 2017). It is believed that exclusive and prolonged parental care is facilitated by more extensive cortico-subcortical connections and by the temporal alignment of physiological and behavioral systems between the caregiver and infant (Feldman, 2012a, 2015). However, much of the existing literature has disproportionately focused on the maternal brain, while investigations into the paternal brain have gained momentum only in recent years. This gap highlights the need for a more balanced exploration of parental neurobiology across caregiving roles and sexes.

The existence of continuities and differences in the evolution of the parental brain between humans and non-human animals has

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encouraged an interdisciplinary approach to its study. Investigations of the parental brain call for contributions from diverse fields, including comparative neuroscience, behavioral biology, psychology, and endocrinology. Following our previous works on the neurobiology of parenting (Carollo et al., 2021a, b, 2023), we adopt a scientometric approach to map the research landscape of the parental brain literature. This systematic overview aims to identify the most impactful studies and outline the main thematic domains of parental brain research.

2. Methods

2.1. Data collection from scopus

For the current analysis, all data were collected from Scopus, a platform that includes a wider collection of indexed journals as compared to other databases (Singh et al., 2023). Data collection was carried out on 13 September 2024 using the search string TITLE-ABS (“parental brain” OR “parental neural” OR “maternal brain” OR “maternal neural” OR “paternal brain” OR “paternal neural”). A total of 656 documents published between 1951 and 2024 were identified (see Supplementary Material 1 for the complete dataset downloaded from Scopus). Titles and abstracts from those documents were next qualitatively inspected to guarantee their relevance in the parental brain literature. This sample of 656 documents is henceforth referred to as “citing documents”.

Subsequently, we used the *bibliometrix* package for R (Aria and Cuccurullo, 2017) to analyze the citing documents, aiming to identify the most influential documents, authors, countries, sources, and keywords in the parental brain literature.

2.2. Data import into CiteSpace

The data import and subsequent scientometric analysis were conducted using CiteSpace (version 6.3.R3 Advanced) (Chen, 2006). A total of 39,302 cited references was identified, of which 38,786 (98.69 %) were deemed valid. A valid reference contains the following seven key pieces of information: author, year of publication, title, source, volume, pages, and DOI (Chen, 2014). Data loss of the current work (i.e., 1.31 %) is considered acceptable and is in line with previous works (e.g., Carollo et al. 2021b).

2.3. Document Co-Citation Analysis (DCA)

A document co-citation analysis (DCA) was next used to map the existing literature on parental brain and identify the most influential publications as well as prevailing research trends (Trujillo and Long, 2018). DCA examines how often two or more documents are cited together (i.e., co-cited) in source articles, based on the premise that frequent co-citations indicate a thematic connection between the documents (Chen et al., 2010; Small, 1973, 1980). This approach is rooted in network theory, where documents are represented as individual nodes, co-citations as connections, and the strength of these connections is determined by the frequency of co-citations.

We also explored various parameter settings to optimize the DCA network by evaluating their impact on the network's final properties (refer to Section 2.4 for a detailed description of the metrics). Specifically, we tested three main node selection methods (i.e., *g*-index, TOP *N*, and TOP *N*%) and their associated scaling factors. Node selection criteria refer to techniques used to decide which documents (i.e., nodes) are to be included in the final network. The *g*-index, a bibliometric measure designed to improve the *h*-index, gives greater weight to highly cited papers, thus providing a deeper understanding of influential documents (Alonso et al., 2009; Egghe, 2006). TOP *N* selects a fixed number (*N*) of the most cited documents, and TOP *N*% includes a specified percentage (*N*%) of the highest-cited publications in the dataset.

In the current work, we conducted a comparative analysis using the

following node selection criteria: *g*-index with scale factor *k* set at 5, 15, and 25; TOP *N* with *N* set at 25 and 50; and TOP *N*% with *N* set at 10 %. The comparison showed that the *g*-index with *k* = 15 generated the most balanced DCA network. This selection was based on the parameter settings' influence on key structural metrics, including modularity (which measures the strength of cluster divisions), silhouette score (which evaluates the homogeneity of the clusters), total node count (reflecting the network's size), and the number of major clusters (indicating meaningful subdivisions within the network). For instance, using the *g*-index with scale factor *k* = 15, the network had 943 nodes, 2944 links, and a modularity of 0.8946, indicating strong and well-defined cluster divisions. The silhouette score of 0.9414 suggested high cluster homogeneity. Importantly, the number of major clusters (10) was optimal for capturing the meaningful subdivisions within the network. We also compared the outcomes when using alternative criteria: TOP *N* and TOP *N*%. With TOP *N* = 25, the network had 515 nodes and 1881 links, but the modularity (0.7677) and silhouette score (0.9078) were lower, suggesting weaker cluster separation and less homogeneity. TOP *N* = 50 yielded a network with 585 nodes, 2156 links, and a modularity of 0.7863, still lower than the *g*-index-based configuration, with silhouette scores indicating slightly weaker cluster quality compared to the *g*-index. The TOP *N*% = 10 configuration yielded results identical to TOP *N* = 50, with both parameter settings generating DCA networks featuring a larger number of clusters (15) compared to the *g*-index-based configuration. This led to increased fragmentation within the network.

The literature search and the generation of the DCA network are presented in the Preferred Reporting Items for Systematic Reviews (PRISMA) flowchart in Fig. 1.

2.4. Network evaluation metrics

DCA properties were assessed using both structural and temporal metrics.

Structural metrics include modularity, silhouette, and betweenness centrality. Modularity measures the degree to which a network can be divided into distinct clusters, with values ranging from 0 to 1 (Chen et al., 2010). Silhouette score reflects the internal homogeneity of clusters and their separation from other clusters, with values ranging from −1 to 1 (Rousseeuw, 1987). Betweenness centrality indicates the extent to which a single document acts as a bridge, connecting two otherwise unrelated documents within the network (Freeman, 1977; Leydesdorff, 2007; Newman, 2005).

Temporal metrics include citation burstness and sigma. Citation burstness, derived from Kleinberg's algorithm, identifies a sudden surge in citations received by a document, indicating that it has gained considerable attention and recognition in its field (Kleinberg, 2002). Focusing on the increase in citations, rather than the overall number of citations, is especially useful for identifying influential works that may not yet have accumulated a large total of citations (e.g., recent publications), but have experienced significant bursts in popularity. These citation bursts often indicate that the work has had a sudden and considerable impact, shaping the direction of future studies in the field. Last, sigma is an index reflecting a document's overall impact on the network and its significance in the field. It is calculated using the formula $(centrality + 1)^{burstness}$, capturing both the document's central role and its citation dynamics (Chen et al., 2009).

3. Results

3.1. Bibliometric analysis on the citing documents

The bibliometric analysis suggested that, on average, documents in the parental brain literature received 33.59 citations, with Strathearn et al. (2009) (total citations on Scopus = 583, average citations per year = 36.40), Feldman (2012b) (total citations on Scopus = 519, average citations per year = 39.90), and Barrett and Fleming (2011) (total

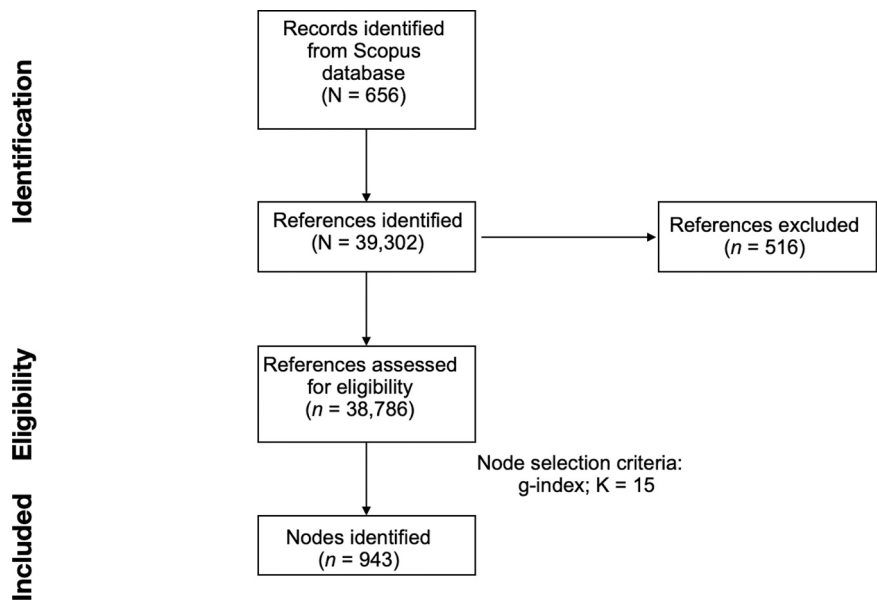


Fig. 1. Preferred reporting items for systematic reviews (PRISMA) flowchart for literature search and references eligibility.

citations on Scopus = 348, average citations per year = 24.90) being the most highly cited works.

In the parental brain literature, a total of 2156 single authors were identified. The most productive authors were Swain JE ($n = 27$ documents), Mayes LC ($n = 18$ documents), and Rutherford HJV ($n = 18$ documents). Analyzing the affiliations of corresponding authors revealed that most publications in the parental brain literature were produced in the United States of America ($n = 188$ documents; Single Country Publications (SCP) = 165, Multiple Country Publications (MCP) = 23), Japan ($n = 26$ documents; SCP = 22, MCP = 4), and Canada ($n = 23$ documents; SCP = 18, MCP = 5).

Documents regarding the parental brain were mostly published in the *Journal of Neuroendocrinology* ($n = 27$ documents), *Hormones and Behavior* ($n = 22$ documents), and *Frontiers in Neuroendocrinology* ($n = 17$ documents).

In the sample of downloaded documents, a total of 1385 authors' keywords were identified. The ten most frequent keywords are presented in Table 1, and the main co-occurrence patterns among these keywords are displayed in Fig. 2.

3.2. Structural properties of the Document Co-Citation Analysis (DCA) network

The DCA network included 943 nodes, representing individual documents, and 2944 links, indicating co-citations between those documents (Fig. 3). Each node had, on average, 3.12 connections, showing a moderate level of interconnectivity within the network. The network

had a modularity score of 0.8946 and an average silhouette score of 0.9414. These metrics indicate that the network was effectively partitioned into distinct research clusters, with minimal overlap. Additionally, the high silhouette score suggests that each research cluster was both well-separated from others and internally cohesive.

Ten major clusters, representing distinct thematic research domains, were identified within the network (see Supplementary Material 2 for the organization of cited documents into thematic clusters). The largest clusters, based on the number of documents they included, were: cluster #0, "Maternal Neuroplasticity" (size = 87 documents, silhouette score = 0.874, mean publication year = 2014); cluster #1, "Parental Responsiveness" (size = 73 documents, silhouette score = 0.947, mean publication year = 2007); and cluster #2, "Maternal Mental Health" (size = 62 documents, silhouette score = 0.967, mean publication year = 2018). Fig. 4 presents the largest clusters within the network, highlighting their relationships over time. The clusters with the highest homogeneity, as indicated by silhouette scores, were: cluster #40, "Lactation" (silhouette score = 0.997, size = 5 documents, mean publication year = 2006); cluster #25, "Dendritic Spine Density and Cognitive-Emotional Adaptations" (silhouette score = 0.996, size = 10 documents, mean publication year = 2005); and cluster #46, "Temporal Resolution" (silhouette score = 0.996, size = 4 documents, mean publication year = 2017). Table 2 provides a summary of the main research clusters identified in the network. For each cluster, we conducted a qualitative review of the documents and replaced automatically generated labels from the log-likelihood ratio (LLR) algorithm with more valid, descriptive labels that better reflect the content of each cluster.

3.3. Most impactful documents in the Document Co-Citation Analysis (DCA) network

In the network, 19 documents (comprising 17 unique entries and 2 repeated entries) showed a sudden increase in citations after publication, marking them as impactful contributions within the DCA network (see Table 3 for a detailed list of these influential documents and their metrics). In terms of citation burst strength, the most influential documents were authored by Bartels and Zeki (2004) (citation burst = 11.46, duration = 4 years), Strathearn et al. (2008) (citation burst = 8.53, duration = 5 years), and Strathearn et al. (2009) (citation burst = 7.90, duration = 6 years). These studies explored various aspects of the parental brain. For instance, Bartels and Zeki (2004) employed

Table 1
Ten most frequent author's keywords appearing in the parental brain literature.

Keyword	Frequency
Pregnancy	84
Maternal behavior	43
Oxytocin	38
fMRI	28
Brain	27
Hippocampus	26
Maternal brain	25
Lactation	24
Postpartum	24
Prolactin	21

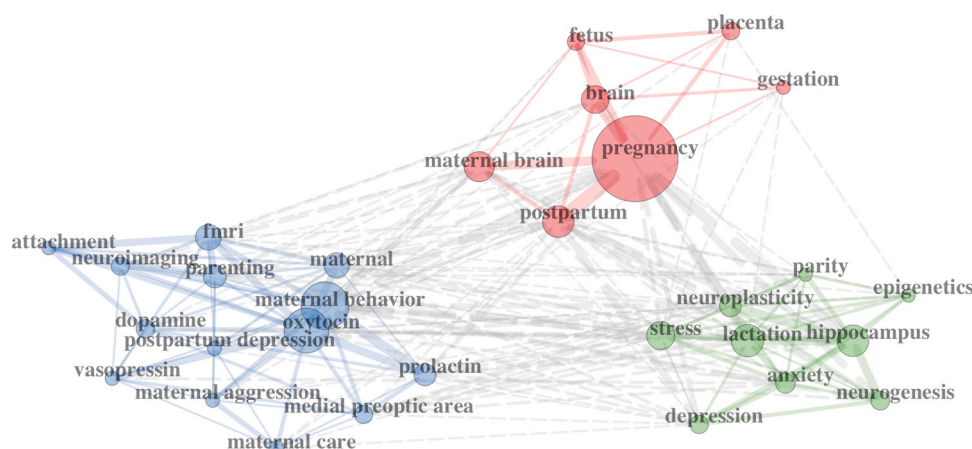


Fig. 2. Co-occurrence analysis performed on the keywords in the parental brain literature. In the resulting network, keywords are visualized as individual nodes, with node size reflecting their degree (i.e., the number of links connecting it to other nodes). Solid links indicate co-occurrences of keywords within the same cluster, and dashed links represent co-occurrences between different clusters. The width of the links indicates the frequency of co-occurrence. The figure highlights three main clusters of co-occurring keywords, each distinguished by a different color.

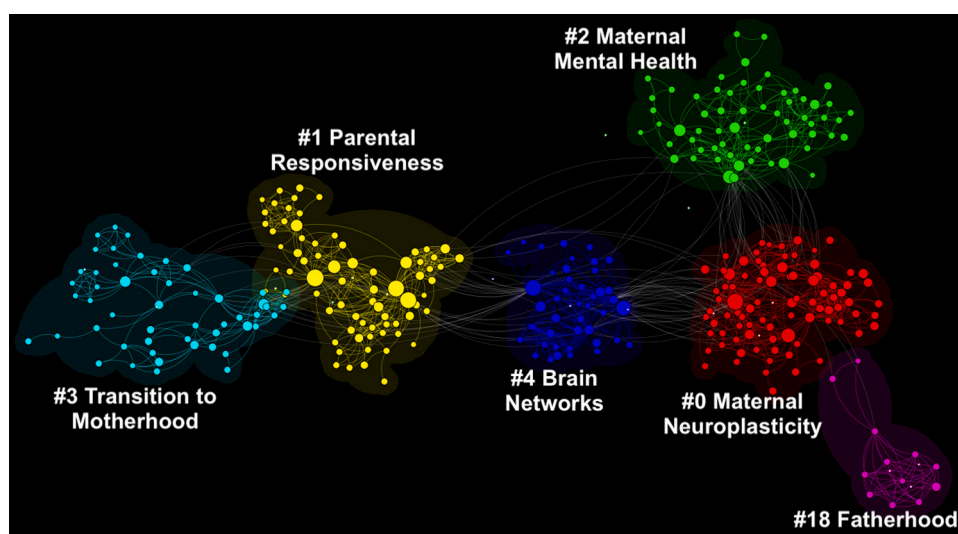


Fig. 3. Document co-citation analysis network of the literature on the parental brain. In the network, documents are represented as single nodes, and co-citations are represented as links. Ten major thematic domains of research were identified. In the figure, the six largest clusters are displayed.

functional magnetic resonance imaging (fMRI) to investigate the neural correlates of maternal attachment, comparing them with those of romantic love. The findings revealed both shared and unique brain regions involved in maternal and romantic love. Their analysis suggested the existence of a push-pull mechanism for both attachment bonds, which relies on *i)* the deactivation of brain areas typically related to negative emotions, avoidance behavior, and social assessment, and *ii)* the activation of reward-related mechanisms. Similarly, [Strathearn et al. \(2008\)](#) utilized an fMRI paradigm to examine the maternal brain's response to infants' facial expressions. Mothers' exposure to their infants' faces activated dopamine-associated reward-processing areas, such as the substantia nigra, indicating a neural reward response linked to viewing infant expressions. Last, [Strathearn et al. \(2009\)](#) used an fMRI paradigm to examine how a mother's attachment style relates to brain reward activation and peripheral oxytocin response to infant cues. Mothers with secure attachment displayed stronger activation in reward-related brain regions, such as the ventral striatum, along with a higher peripheral oxytocin response to infant contact at 7 months. Overall, these impactful studies highlight the role of dopamine and oxytocin pathways in reinforcing and promoting mother-infant

attachment.

4. Discussion

Research on neurobiological mechanisms underlying parenting has expanded significantly. This systematic review of the scientific literature in parental brain uses a data-driven approach to map the structure of knowledge, identify key thematic research domains, and highlight impactful publications. Our scientometric analysis revealed 10 thematic domains in the parental brain literature, alongside 17 impactful publications. These influential studies predominantly focus on investigating the neural substrates that drive parental behaviors, shedding light on brain mechanisms that support caregiving and attachment.

In the following section, we present a detailed description of each research cluster, ordered chronologically from the oldest (average year of documents' publication = 2005) to the most recent (average year of documents' publication = 2018) based on the clusters' mean publication year. We begin with quantitative data, discussing each cluster's characteristics such as coverage (i.e., the number of references in the cluster cited by a citing document) and global citation score (GCS; i.e., the total

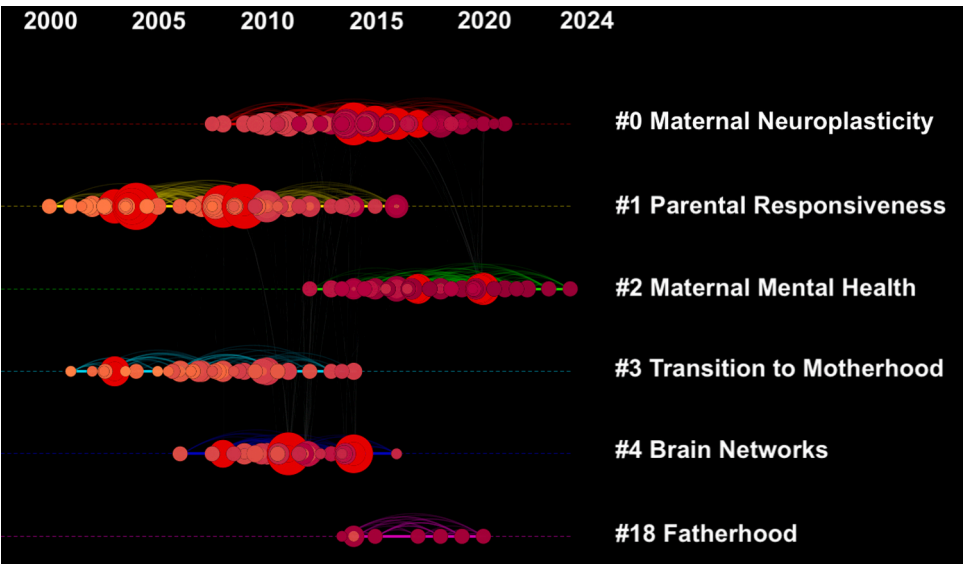


Fig. 4. Timeline view of the six largest clusters identified in the document co-citation analysis network of the literature on the parental brain, illustrating the evolution of key research themes over time.

Table 2
Metrics for the ten thematic clusters of research identified in the network. Each cluster shows its ID, size, silhouette, average year of publication for its documents, log-likelihood ratio (LLR) label, and the authors' suggested label. We suggested an alternative label after a qualitative review of the cluster documents, aiming to provide a more valid description of the clusters' content.

ID	Size	Silhouette	Mean Year	LLR Label	Authors' Suggested Label
0	87	0.874	2014	repeated stress	maternal neuroplasticity
1	73	0.947	2007	human parental brain	parental responsiveness
2	62	0.967	2018	functional change	maternal mental health
3	51	0.955	2007	social maternal phenotype	transition to motherhood
4	44	0.968	2011	cerebral area	brain networks
18	12	0.989	2016	role	fatherhood
25	10	0.996	2005	meaning	dendritic spine density and cognitive-emotional adaptations
29	9	0.983	2012	parental behavior	experience and innateness
40	5	0.997	2006	many mouth	lactation
46	4	0.996	2017	adult attachment	temporal resolution

number of citations received by a citing document in Scopus). Clusters are then explored qualitatively to provide deeper insights into the thematic content and significance of each in the context of the larger neurobiological research literature on parenting.

4.1. Cluster #25: dendritic spine density and cognitive-emotional adaptations (2005)

The earliest thematic cluster of research in the parental brain literature was shaped by two citing documents, authored by [González-Mariscal and Kinsley \(2009\)](#) (coverage = 6, GCS = 10) and [Crozier et al. \(2009\)](#) (coverage = 5, GCS = 0). These works review how peptide and steroid hormones drive neuroplasticity and structural changes in the maternal brain, particularly in dendritic spines. These spines, which are crucial for receiving synaptic inputs, undergo significant changes in density and morphology due to hormonal (e.g.,

estrogen, estradiol, and progesterone) fluctuations during pregnancy and the postpartum period. For instance, pregnancy and lactation alter dendritic spine density and complexity in the maternal hippocampus, with these changes further influenced by reproductive history ([Crozier et al., 2009](#)). Specifically, reproductive history modulates the persistence of dendritic spines, as evidenced by the transient nature of increased spine density in primiparous females after weaning, compared to the sustained spine density observed in multiparous females ([Pawluski and Galea, 2006](#)). Similarly, gonadal hormones affect spine density in other brain regions, such as the amygdala and prefrontal cortex. These effects on the prefrontal cortex extend beyond motherhood, as structural alterations have been observed in first-time and experienced marmoset fathers ([Kozorovitskiy et al., 2006](#)).

The plasticity of the maternal brain is not limited to structural changes but also has profound cognitive and emotional consequences. Studies have shown significant differences in spatial learning and exploratory/emotional behaviors between parous and nulliparous female rats ([Love et al., 2005](#)), reflecting the adaptive significance of neuroplasticity for environmental responsiveness and caregiving.

Maternal memory, defined as the long-term retention of maternal responsiveness following prior interactions with offspring, is another key area shaped by maternal brain plasticity. [Li and Fleming \(2003\)](#) explored the role of the nucleus accumbens in this process, demonstrating that lesions to the shell (but not the core) subregion made before or shortly after pup exposure significantly impair maternal memory. This finding highlights the nucleus accumbens shell as a critical region for consolidating maternal memory. Additionally, [Graham et al. \(2006\)](#) found that corticosterone enhances maternal memory and initial maternal behaviors in postpartum rats.

4.2. Cluster #40: lactation (2006)

Cluster #40 focuses on research related to the energetic demands of lactation and hormonal mechanisms involved in energy regulation during and after pregnancy, particularly as evidenced in animal preparations. The main citing document in this cluster, authored by [Woodside et al. \(2012\)](#) (coverage = 5, GCS = 44), addresses metabolic adaptations that occur in pregnant and lactating rats, emphasizing changes in energy storage and usage. According to the authors, these adaptations are largely mediated by fluctuations in metabolic hormones like leptin, which plays a critical role in managing increased food intake (hyperphagia) during pregnancy – a process also explored in [Augustine and](#)

Table 3
Summary metrics of the seventeen unique documents with a citation burst.

Reference	Citation Burstness	Publication Year	Burst Begin	Burst End	Duration (years)	Centrality	Sigma
Bartels and Zeki (2004)	11.46	2004	2008	2012	4	0.02	1.32
Strathearn et al. (2008)	8.53	2008	2011	2016	5	0.06	1.70
Strathearn et al. (2009)	7.90	2009	2011	2017	6	0.03	1.27
Dulac et al. (2014)	7.55	2014	2016	2022	6	0.03	1.26
Atzil et al. (2011)	7.54	2011	2012	2019	7	0.07	1.66
Bridges (2015)	7.40	2015	2017	2020	3	0.02	1.16
Rilling and Young (2014)	7.30	2014	2016	2021	5	0.02	1.12
Nitschke et al. (2004)	6.73	2004	2008	2012	4	0.01	1.08
Hoekzema et al. (2020)	6.21	2020	2020	2024	4	0.02	1.10
Numan and Insel (2006)	6.08	2003	2008	2011	3	0.02	1.11
Hoekzema et al. (2017)	5.16	2017	2020	2024	4	0.01	1.07
Luders et al. (2020)	5.08	2020	2021	2024	3	0.02	1.10
Kim et al. (2016)	5.03	2016	2019	2024	5	0.01	1.08
Shingo et al. (2003)	4.89	2003	2007	2011	4	0.01	1.05
Numan (2020)	4.51	2020	2021	2024	3	0.01	1.05
Ranote et al. (2004)	4.41	2004	2008	2011	3	0.01	1.02
Noriuchi et al. (2008)	4.40	2008	2014	2016	2	0.00	1.00

Grattan (2008), which highlights leptin’s specific role in these energy shifts. In addition to leptin, the role of prolactin – a hormone central to lactation–has been a focus of investigation in the context of lactational physiology. Kokay et al. (2006) proposed that prolactin may influence the activity of oxytocin neurons, which are essential in facilitating milk ejection and supporting the overall lactational response.

4.3. Cluster #1: parental responsiveness (2007)

The main citing documents in cluster #1 were authored by Swain et al. (2011) (coverage = 19, GCS = 80), Swain (2011) (coverage = 17, GCS = 168), and Atzil et al. (2011) (coverage = 16, GCS = 279). This cluster centers on understanding how the parental brain responds to (or, in some cases, neglects) infant-related cues, such as crying, and how the stress response system mediates these emotional and motivational processes, thereby encouraging sensitive caregiving. Swain et al. (2011) highlighted the role of brain circuits associated with social cognition, which interact with the endocrine system to manage stress and facilitate adaptive parental behavior in response to environmental demands. This argument was further supported by Swain (2011), who identified key brain pathways (i.e., the hypothalamic-midbrain-limbic-paralimbic-cortical circuits) that are activated in response to infant stimuli, highlighting how these systems underlie sensitive parental responses.

Additionally, Kim et al. (2010a) provided evidence of structural changes in the maternal brain, with increased gray matter volume in the midbrain linked to mothers’ positive perceptions of infants. Similarly, the study by Strathearn et al. (2009) linked maternal attachment behaviors to activation within oxytocin-related areas of the hypothalamus and pituitary. These studies suggest that neural plasticity and hormonal fluctuations are critical for enhancing maternal sensitivity to infant cues and needs.

4.4. Cluster #3: transition to motherhood (2007)

In cluster #3, the major citing documents are authored by Lambert (2012) (coverage = 8, GCS = 29), Stolzenberg and Champagne (2016) (coverage = 7, GCS = 83), and Atzil et al. (2012) (coverage = 7, GCS = 184). The documents in this cluster focus on the neurobiological changes associated with the transition to motherhood (e.g., Stolzenberg and Champagne 2016), especially examining changes in social processes and social cognition. These changes support adaptive responses in mothers, characterized by enhanced cognitive flexibility, emotional regulation, and social attentiveness (Lambert, 2012).

A significant portion of the documents in this cluster aims to identify mechanisms underlying parent-child bonding and to compare them with mechanisms of bonding formation more generally, such as in romantic

relationships. For example, Numan and Young (2016) observed that the amygdala and the nucleus accumbens-ventral pallidum circuits play roles in both mother-infant and romantic bonds. Dopamine and oxytocin in the nucleus accumbens promote synaptic plasticity, enabling social stimuli to activate the nucleus accumbens-ventral pallidum attraction circuits and thus support social attraction over the long term. Conversely, the medial preoptic area (mPOA) has been identified as a critical region for maternal behavior. Among the nuclei in the preoptic area (POA) of the brain – areas involved in regulating functions such as blood osmolality, temperature, sleep, and ovulation – the mPOA specifically contributes to parental behavior across mammalian species (Fisher, 1956; Kuroda and Numan, 2014; Numan, 1974; Numan and Insel, 2006). With respect to the mPOA’s role in fostering sociability in the mother-child bond, studies have investigated gene expression in this area as a basis for understanding social deficits in mental health disorders such as autism spectrum disorder, bipolar disorder, and schizophrenia (e.g., Driessen et al. 2014; Eisinger et al. 2014). These studies identified novel genes shared between the postpartum mPOA (associated with increased sociability) and mental health disorders (linked to reduced sociability). Thus, researchers conclude that the activity of these genes may influence social behavior in opposite directions under varying conditions.

Another important mechanism underlying adaptive parental care and coordination is bio-behavioral synchrony, which refers to the coordination of biological and behavioral responses between parent and child (Atzil et al., 2011). In their study, Atzil et al. (2011) provided preliminary evidence of interpersonal brain synchrony between caregivers (both mothers and fathers) in response to infant cues. The findings revealed synchrony in social-cognitive networks involved in empathy and social cognition. Additionally, the authors observed distinct patterns between mothers and fathers: mothers showed higher amygdala activation, which correlated with plasma oxytocin levels, whereas fathers demonstrated greater activation in social-cognitive circuits, correlating with plasma vasopressin.

4.5. Cluster #4: brain networks (2011)

The main citing documents in cluster #4 include works by Feldman (2015) (coverage = 16, GCS = 289), Piallini et al. (2015) (coverage = 16, GCS = 22), and Swain et al. (2014) (coverage = 14, GCS = 223). Studies in this cluster map brain networks that enable caregivers to provide sensitive and attuned care to infants. Expanding on the findings in cluster #3, Feldman (2015) outlined the human parental caregiving network, which integrates evolutionarily preserved brain structures that facilitate caregiving across mammalian species along with more recently developed networks. Feldman suggested that parenting has played a

significant role in the evolution of complex social functions that enhance infant survival.

In terms of conserved caregiving mechanisms, research highlights the amygdala and the reward circuit as central to maintaining parental vigilance for infant safety and reinforcing the parent-infant attachment bond (Swain et al., 2014). In the study by Caria et al. (2012), activations in the reward system were observed even in non-parent humans when exposed to unfamiliar human infant faces. Another evolutionarily preserved feature is heightened brain plasticity in parents, allowing dynamic reorganization of the parental brain in reaction to caregiving stimuli (Kim et al., 2010a). Oxytocin also plays a key role in subcortical circuits that support caregiving across mammalian species, contributing to socio-emotional functions in humans such as empathy, social cohesion, and interpersonal understanding (Rocchetti et al., 2014; Sokolowski and Corbin, 2012).

Unlike other mammalian care circuits, the human parental caregiving network integrates these subcortical structures with insular, cingulate and fronto-temporo-parietal networks (Bornstein et al., 2017; Feldman, 2015; Rocchetti et al., 2014). The fMRI meta-analysis conducted by Rigo et al. (2019) revealed that images of one's own child, compared to images of non-related children, tend to activate the left hemisphere more than the right. Additionally, greater activation was observed in the left ventro-lateral prefrontal cortex, insula, amygdala, bilateral striatum, and midbrain. While rodent models are frequently used in parental behavior studies, the human parent-infant bond is exclusive and highly individualized, a pattern found in few other mammals. In non-human mammals, the exclusivity of the parent-infant bond is often based on olfactory signals (Corona and Lévy, 2015), whereas human affiliative bonds are formed through multimodal cues, memory, and associative processes (Broad et al., 2006). A key factor in this bonding process is bio-behavioral synchrony (attunement, coregulation), which involves the mutual regulation of physiology and behavior between parent and infant (Bornstein, 2013; Bornstein and Esposito, 2023). This synchrony drives brain plasticity, enabling caregivers' brains to attune to their infants' specific signals (Feldman, 2015). Preliminary research suggests that mother-child neural synchrony may be impaired by parental stress (Azhari et al., 2019).

4.6. Cluster #29: experience and innateness (2012)

Cluster #29 explores neurobiological and hormonal mechanisms underlying parental behavior, focusing on the lasting effects of maternal experience and sexual dimorphism in caregiving. This cluster is shaped by two key documents: González-Mariscal et al. (2017) (coverage = 6, GCS = 10) and Zilkha et al. (2017) (coverage = 6, GCS = 20). González-Mariscal et al. (2017) examined mammalian maternal behavior, highlighting the hormonal and neural mechanisms involved in initiating and ending specific caregiving actions. A central focus is the impact of maternal care on the mothers' brain, where neuroanatomical changes in experienced mothers lead to more efficient caregiving behavior, potentially enhancing cognitive functions and reducing fear and anxiety. Similarly, Bridges (2016) reviewed comparative studies showing that reproductive experiences significantly reshape a female's biological state, including neuroendocrine and immunological processes. The author argued that experiences of parity and motherhood alter hormone levels, neural receptor gene expression, and neural processes as well as glial support, leading to profound, long-term changes in the adult female brain. In parallel, Zilkha et al. (2017) explored the neurobiological mechanisms of both maternal and paternal care, focusing on rodent models. While parental care is evolutionarily conserved across species to promote offspring survival, Zilkha et al. (2017) highlighted considerable variability in caregiving behaviors between sexes across species. Focusing on rodent models, Zilkha et al. (2017) argued that, although both sexes share some neural circuits for parental care (e.g., olfactory bulbs, mPOA, amygdala), closer observations of these (and other) brain regions revealed sex-specific properties

(e.g., Scott et al. 2015). For instance, Wu et al. (2014) observed that optogenetic stimulation of galanin neurons in the mPOA increased parental care in both male and female sexually naive mice, though pup retrieval behavior was induced only in females. Sex-specific properties are also observed in the human parental brain (De Pisapia et al., 2013; Esposito et al., 2015a; Messina et al., 2016). Furthermore, selective responses based on the sex of the caregiver have been found in the neural responses of infants in response to infant-directed speech (Sulpizio et al., 2018). However, as Wu et al. (2014) noted, identifying sexual dimorphism in the neural circuitry underlying parental behavior remains methodologically challenging. This is because most studies in this field focus predominantly on females and research on male parental care often centers on biparental species, which are not representative of typical sexual dimorphism in most mammals. Consequently, it is often unclear whether specific circuits are female-exclusive or merely unexamined in uniparental males.

4.7. Cluster #0: maternal neuroplasticity (2014)

The main citing documents in cluster #0 are authored by Leuner and Sabihi (2016) (coverage = 22, GCS = 70), Slattery and Hillerer (2016) (coverage = 2, GCS = 23), and Pawluski et al. (2016) (coverage = 22, GCS = 95). Overall, these documents focus on neuroplastic changes that occur in the maternal brain across the peripartum period. One mechanism that underlies the maternal brain's neuroplasticity is neurogenesis (Leuner and Sabihi, 2016). Neurogenesis is the process by which new neurons are generated from neural stem cells and progenitor cells. In most adult mammals, neurogenesis occurs in the dentate gyrus of the hippocampus and in the olfactory bulbs, whose new cells typically originate from the sub-ventricular zone (Leuner and Sabihi, 2016). The review article by Leuner and Sabihi (2016) suggested that neurogenesis in the dentate gyrus and the subventricular zone is altered in both mothers and fathers during the peripartum period. In the dentate gyrus, evidence regarding the inhibition of cell proliferation during pregnancy is conflicting (Kim et al., 2010b; Shingo et al., 2003). However, studies in rat models show a significant reduction in cell proliferation during the early to mid-postpartum period compared to nulliparous females (Hillerer et al., 2014; Pawluski and Galea, 2007). In the subventricular zone, cell proliferation in rats increases during late pregnancy but not in the early stages, whereas an opposite pattern is observed in mice (Furuta and Bridges, 2005; Shingo et al., 2003). Overall, studies suggest that maternal hippocampal neurogenesis depends in part on the decrease in the hypothalamic-pituitary-adrenal (HPA) axis responsiveness to external stressors in the peripartum period (Hillerer et al., 2014; Pawluski et al., 2016; Slattery and Hillerer, 2016).

4.8. Cluster #18: fatherhood (2016)

Cluster #18 focuses on the neurobiological mechanisms of paternal responsiveness, examining both brain function and hormonal influences that support sensitive fathering. The two citing documents of this cluster were authored by Giannotti et al. (2022) (coverage = 10, GCS = 8) and by Sobral et al. (2022) (coverage = 8, GCS = 5). Documents in this cluster underscore that, whereas maternal responsiveness has been widely studied, there is a significant gap in understanding the neurobiological mechanisms that underlie paternal sensitivity to infant cues, especially in the context of pregnancy and the postpartum period. Sobral et al. (2022) built on this theme by emphasizing the neurofunctional and neuroendocrinal changes that occur in fathers during the postpartum period. They reviewed evidence showing that paternal brains undergo adaptations in networks related to empathy, approach motivation, emotional processing, mentalizing, emotion regulation, dorsal attention, and default mode networks. Alongside these functional changes, shifts in hormone levels – including testosterone, oxytocin, prolactin, and cortisol – also play a key role in preparing fathers for responsive caregiving. Giannotti et al. (2022) presented a comprehensive review of the

role of parental involvement in shaping paternal sensitive responsiveness and neurobiological activations. Early research showed differences between father and mother neural activation in response to infant cues (e.g., [Rajhans et al. 2019](#)), but most studies have not taken the variability related to paternal involvement into account. The studies reviewed by [Giannotti et al. \(2022\)](#) suggest that paternal involvement, which depends on caregiving experience and not on pregnancy and childbirth, modulates both hormonal and neural pathways associated with paternal behaviors. For example, elevated cortisol levels after interacting with newborns have been linked to greater future involvement in indirect childcare and play, although such increases may also reflect early paternal role adjustment and potentially less sensitive care over time ([Bos et al., 2018](#); [Kuo et al., 2018](#)). Prolactin levels, conversely, show a short-term decline in fathers more engaged in routine care ([Gettler et al., 2011](#); [Storey et al., 2020](#)). Regarding neural activity, caregiving involvement has been associated with increased activation of the ventral tegmental area and anterior insula, reflecting optimal arousal for engaged parenting as well as coactivation of subcortical and cortical networks in primary-caregiving fathers ([Abraham et al., 2014](#); [Mascaro et al., 2013,2014](#)). Moreover, as observed by [Kim et al. \(2015\)](#), early paternal engagement and positive perceptions of parenthood are associated with positive socioemotional development in children.

4.9. Cluster #46: temporal resolution (2017)

Cluster #46 has one citing document authored by [Lowell et al. \(2023\)](#) (coverage = 4, GCS = 13). In this article, the authors used event-related potentials (ERPs) to investigate the time course of maternal responsiveness to infant cues as a function of adult attachment status. Secure and insecure mothers differ in the speed with which they process infant stimuli rather than the strength of their neural responses. Specifically, secure mothers were significantly faster to orient to infant cries (N100), structurally encode their infant's face (N170), and attend to infant faces (P300). Similar studies, such as [Leyh et al. \(2016\)](#), observed differences in the neural response amplitude in the N170 component between secure and insecure mothers when exposed to negative infant emotions.

Furthermore, the electrophysiological study by [Bornstein et al. \(2013\)](#) compared maternal responses to their own versus unfamiliar children. Primipara mothers exhibited similar early-wave responses (N170) to both their own and unfamiliar infants' faces, but their late-wave activity (N/P600) differentiated between the two stimuli. In addition, spectral power in three EEG bands (delta, theta, and gamma) in mothers was found to vary between exposures to images of their own versus unfamiliar children ([Esposito et al., 2015b](#)). Similar evidence was found in infants, showing differential brain dynamics in response to exposure to familiar (mother's) versus unfamiliar faces ([Mash et al., 2013](#)).

4.10. Cluster #2: maternal mental health (2018)

The main citing documents of cluster #2 are authored by [Pawluski \(2024\)](#) (coverage = 12, GCS = 0), [Martinez-Garcia et al. \(2021\)](#) (coverage = 10, GCS = 22), and [Nehls et al. \(2024b\)](#) (coverage = 9, GCS = 3). The documents in this cluster primarily examine relations between the transition to parenthood and parents' mental health. Most research in this area emphasizes these neurobiological changes in women (e.g., [Pawluski 2024](#); [Voldsbekk et al. 2021](#)).

Studies in this cluster examine factors that increase the risk of postpartum depression in mothers (e.g., [Nguyen et al. 2019](#)). Postpartum depression generally emerges within the first 4–6 weeks after childbirth and is thought to result from neuroplastic changes and peripartum hormonal fluctuations ([Nehls et al., 2024a](#)). Specifically, the HPA axis appears to play a critical role in the dysregulation of perinatal mental health ([Dickens and Pawluski, 2018](#)). Dysregulation of the HPA

axis not only heightens the risk for perinatal mental health disorders but also contributes to impaired maternal behaviors. According to [Sanson et al. \(2024\)](#), maternal caregiving behaviors are typically supported by the up-regulation of neuropeptide systems involving oxytocin, vasopressin, and prolactin, along with the down-regulation of the corticotropin-releasing factor system. However, deviations from this regulatory pattern can lead to impaired maternal behaviors. For instance, parenting stress, which is associated with up-regulation of the corticotropin-releasing factor system, disrupts parental behaviors and affects neurobiological adaptations characteristic of parenthood ([Pawluski, 2024](#)).

4.11. Overall temporal evolution of the literature

Over time, research on the parental brain has evolved from an early focus on the structural changes in the brain during pregnancy and lactation (dendritic spine changes, hormonal influences on brain regions like the hippocampus and amygdala) to a deeper exploration of the neurobiological, hormonal, and cognitive mechanisms that support adaptive, real-time caregiving. Initially, studies were largely based on animal models, where research focused on understanding how pregnancy and lactation induced structural changes in the brain, especially regarding hormonal effects on brain regions involved in learning, emotion, and spatial navigation. These early animal-based studies explored how the hormonal fluctuations during pregnancy (e.g., estrogen, progesterone) and lactation influenced brain areas like the hippocampus, amygdala, and prefrontal cortex, which are crucial for emotional regulation, spatial learning, and caregiving behavior. The focus was initially on the maternal brain, examining how pregnancy and lactation influence brain structures and caregiving behaviors. Later, research expanded to include paternal involvement, highlighting the shared and distinct neural mechanisms in fathers. Research also began to explore the relationship between mental health, particularly postpartum depression, and caregiving. As the research progressed, there was a shift towards understanding complex brain networks, with a focus on how experiences shape brain structures and networks over time, enabling more flexible and responsive caregiving. This broader understanding now includes how neuroplasticity, hormonal shifts, and real-time brain responses to infant cues contribute to effective and adaptive parenting.

5. Conclusion

The current study used a scientometric approach (as in [Carollo et al., 2021a, b, 2023](#)) to provide a data-driven overview of 75 years of scientific literature on the parental brain. The analysis revealed that works by [Bartels and Zeki \(2004\)](#), [Strathearn et al. \(2008\)](#), and [Strathearn et al. \(2009\)](#) significantly influenced the development of subsequent research. These studies examined the parental brain's responsiveness to infant cues, linking responsiveness with maternal attachment style. Additionally, [Bartels and Zeki \(2004\)](#) introduced a novel perspective by examining both the continuity and distinctiveness of the neurophysiological foundations of the mother-infant bond compared to other human attachments, such as romantic relationships. Moreover, the present review revealed that the literature on the parental brain has followed a progressive trajectory, moving from foundational studies on the neurobiological bases of maternal memory, particularly in rodent models, toward a more complex understanding of the human parental caregiving network ([Feldman, 2015](#)), which facilitates adaptive and sensitive caregiving. In this network, the mPOA plays a central role ([Carollo et al., 2021a](#); [Numan, 1974](#)). As this field has advanced, studies have increasingly addressed changes associated with the transition to fatherhood, differentiating between changes driven by the timing of pregnancy and birth-related hormones and those influenced by factors such as parental involvement and environmental context ([Giannotti et al., 2022](#)). Research has also begun to explore how dysregulations in these neurobiological transitions might augment risks for mental health

conditions, including postpartum depression. The studies reviewed here portray the parental brain as a dynamic, adaptive network shaped by both evolutionarily conserved structures and uniquely human social-cognitive circuits, with bio-behavioral synchrony serving as a key interpersonal mechanism that reinforces the specificity of adult attachments (Feldman, 2017). However, the literature remains disproportionately focused on the maternal brain, with relatively fewer studies investigating the paternal brain. While research on fatherhood has gained momentum in recent years, much remains to be explored regarding the neurobiological underpinnings of paternal caregiving.

Abbreviations

The following abbreviations are used in this manuscript:

DCA	Document Co-Citation Analysis
ERP	Event-Related Potentials
fMRI	Functional Magnetic Resonance Imaging
GCS	Global Citing Score
HPA	Hypothalamic-Pituitary-Adrenal
LLR	Log-Likelihood Ratio
MCP	Multiple Country Publications
PRISMA	Preferred Reporting Items for Systematic Reviews
POA	Preoptic Area
mPOA	Medial Preoptic Area
SCP	Single Country Publications

CRediT authorship contribution statement

Gianluca Esposito: Conceptualization, Supervision, Writing – review & editing. **Alessandro Carollo:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Lucrezia Torre:** Writing – original draft, Writing – review & editing. **Marc H. Bornstein:** Writing – review & editing.

Declaration of Competing Interest

The authors declare no conflict of interest.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neures.2025.03.002.

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