Grandmaternal caregiving is associated with a distinct multi-voxel neural representation of grandchildren in the parental motivation circuit

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Abstract

Grandmothers enhance grandchild survival and maternal health through caregiving. Comparative evidence suggests that human grandmotherhood reflects a unique life history strategy promoting the inclusive fitness of post-reproductive females. Despite its evolutionary importance, the proximate neural mechanisms supporting grandmaternal caregiving remain unclear. This study uses functional magnetic resonance imaging (fMRI) and multivariate approaches to investigate how grandmaternal brains encode information about grandchildren and translate it into caregiving. Forty-seven grandmothers (age = 59.1 ± 7 years) completed an fMRI task viewing photos of a grandchild, the grandchild's parent, unfamiliar individuals, and nonhuman objects. Multi-voxel activation patterns associated with these stimuli were analyzed using representational similarity analysis, focusing on the hypothalamic and mesolimbic regions critical for mammalian parenting. Results reveal that grandchildren had the most distinct multi-voxel pattern of activation within these regions, potentially reflecting the grandmothers' motivational readiness to engage in grandmaternal caregiving. Indeed, greater neural dissimilarity between the grandchild and other social categories correlated with higher self-reported affection and supportive behaviors towards grandchildren, particularly in paternal grandmothers. Our findings provide novel insights into the mechanisms of grandmaternal caregiving that enhances inclusive fitness.

Keywords: grandmothers; caregiving; motivation; grandmother hypothesis; multivariate analysis

Introduction

Grandmothers serve a crucial role as alloparents across traditional and industrialized societies, offering nutritional, emotional, and financial support to parents while assisting with daily caregiving tasks (Hawkes *et al.*, 1998; Hrdy, 2005). Grandmaternal investment positively impacts grandchildren's survival, sociocognitive development, and educational attainment while also enhancing maternal health and fertility (Rilling *et al.*, 2021). These findings form the basis of the "grandmother hypothesis," which suggests that human grandmotherhood evolved to increase inclusive fitness after reproductive senescence (Hawkes and Coxworth, 2013). Comparative evidence further bolsters this theory, as extended postreproductive lifespans and grandmaternal caregiving are rare outside humans (Kramer, 2010).

If grandmotherhood was selected for its adaptive benefits, proximate mechanisms likely evolved to support this role. For instance, information about genetic or affinal kin, such as grandchildren and their parents, may be perceived as highly salient and rewarding stimuli and encoded in the brain as such. Many grandmothers indeed report the motivational significance and rewarding nature of alloparenting (Moore and Rosenthal, 2015). However, our understanding of the brain circuits implicated in grandmaternal caregiving, and the specific neural signatures predictive of grandmaternal caregiving behaviors, remains limited.

Caregiving in humans is a complex, multi-faceted phenomenon, likely orchestrated by multiple functionally distinct neural systems (Rilling, 2013). Among these, the mesolimbic dopamine and hypothalamic systems—evolutionarily preserved

circuits that regulate parental motivation and behavior across mammalian species—are considered promising candidates for these mechanisms. In rodents, the medial preoptic area (MPOA) regulates caregiving behaviors by processing hormonal inputs such as oxytocin and prolactin and modulating reward-related circuits such as the ventral tegmental area (VTA), nucleus accumbens (NAcc), and ventral pallidum (VP) (Numan and Stolzenberg, 2009). Similarly, in humans, infant cries and smiles elicit increased activation in the hypothalamus and VTA, with stronger responses linked to stronger maternal attachment (Strathearn et al., 2009). Studies using images of older offspring have also found increased activation in the midbrain (e.g. VTA) and striatal regions (e.g. NAcc), supporting the broader role of the parental motivation circuit in processing caregiving-related stimuli (Bartels and Zeki, 2004; Stoeckel et al., 2014).

Emerging evidence suggests these systems may also underpin a broader range of parental behaviors, such as paternal or allomaternal care. Lesions in the MPOA disrupt paternal behaviors in California mice (Lee and Brown, 2007), while optogenetic stimulation of galanin-expressing MPOA neurons triggers caregiving behaviors, such as pup grooming, even in virgin male rats that typically avoid pups (Wu et al., 2014). In prairie voles, oxytocin in the NAcc drives allomaternal care by nonreproductive females (Olazabal and Young, 2006). In humans, first-time fathers show increased activation in the hypothalamus, NAcc, and VTA when viewing infant images (Swain et al., 2014), with stronger VTA activation among those more engaged in caregiving (Mascaro et al., 2014). These findings suggest that the mesolimbic and hypothalamic circuits may facilitate grandmaternal caregiving by enhancing affiliative motivations toward grandchildren.

A previous functional magnetic resonance imaging (fMRI) study from our lab provided preliminary evidence for this, showing that the MPOA, NAcc, VP, and VTA increased activation when grandmothers viewed photos of their grandchildren compared to familiar adults or unknown children (Rilling et al., 2021). However, this initial study also had limitations. Most notably, it relied solely on univariate methods, falling short of capturing distributed patterns of neural activity and their hierarchical organization. These multi-voxel neural representations may contain additional, more nuanced information than average BOLD signal amplitudes (Popal et al., 2019), such as whether the grandmaternal brain represents grandchildren and their parents with greater specificity than other social categories. Potentially reflecting the reduced sensitivity of the univariate approach, we previously found no significant link between grandmaternal caregiving and average BOLD responses to grandchildren in the hypothalamic and mesolimbic circuits (Rilling et al., 2021). Identifying higher-order representational structures of grandchildren and other social categories could more sensitively reveal neural signatures of grandmaternal caregiving that univariate analyses may have overlooked.

This study aimed to address gaps in understanding the neural basis of grandmaternal caregiving by applying representational similarity analysis (RSA), a multivariate method that quantifies pairwise dissimilarity between spatial patterns of neural activity. RSA generates a representational dissimilarity matrix (RDM), showing the degrees of alignment in multi-voxel neural activities associated with task conditions or stimulus types. The neural RDM can be then compared to theoretical models to test specific hypotheses about the representational structures in a more principled way than other multivariate approaches based on classification accuracy (Popal et al., 2019). RSA has been widely used to identify fine-grained neural representations of features like face identity, relationship closeness, and biological classes, often

revealing effects undetected by univariate approaches (Connolly et al., 2012; Chavez and Heatherton, 2015; Tsantani et al., 2021).

In this study, we applied RSA to data from our previous fMRI experiment (Rilling et al., 2021), examining how grandchildren are represented in the hypothalamic and mesolimbic circuits and whether these representations predict various facets of grandmaternal caregiving. Grandmothers of diverse backgrounds performed a face perception task, viewing photos of their own grandchild (OGC), alongside other individuals varying in age, familiarity, or kinship. Grandmothers also completed diverse self-report measures of caregiving, which were then analyzed with the RSA outputs—specifically, the neural dissimilarity between grandchildren and other categories in the hypothalamic and mesolimbic regions. Lastly, we evaluated if the results of RSA and univariate analysis differentially explained grandmaternal caregiving. Drawing on the Grandmother Hypothesis, we predict that grandchildren and their parents will induce distinct multi-voxel activation patterns compared to other social categories **(Prediction 1)**. We also predict that such distinct multi-voxel neural representation of grandchildren will translate to the levels of caregiving engagement by grandmothers **(Prediction 2)**.

Materials and methods
Participants

Fifty females (Mean age = 59.3 ± 7.8 years) with at least one biological grandchild aged 3–12 years were recruited through social media and flyers. Participants with MRI contraindications, neurological disorders, or severe psychiatric conditions were excluded. Depression was permitted to ease recruitment but was not clinically significant in any participant **(SI-3)**. Three participants who were spending no time with grandchildren were excluded, leaving a final sample of 47 (Table 1).

Focal grandchildren and adult parents

Fifty dyads of grandchildren (Mean age = 6.8 ± 2.8 years) and same-sex parents (Mean age = 34.4 ± 5.9 years) were recruited

Table 1. Demographic characteristics of grandmothers

Demographic (**N** = 47)	Categories	N	%
Race	Black	21	44.7
	White	23	48.9
	Hispanic	2	4.3
	Mixed-race	1	2.1
Grandmother lineage	Maternal	28	59.6
	Paternal	19	40.4
Relationship to adult parent	Biological	30	63.8
	In-law	17	36.2
Living arrangement	Live with grandchildren	10	78.7
	Live separate from grandchildren	37	21.3
Work status[a]	Full-time	14	29.8
	Part-time	9	19.1
	Retired	15	31.9
	Working at home	5	10.6
Household annual income	$10 000–$49 999	22	46.8
	$50 000–$99 999	15	31.9
	$100 000–$14 999	7	14.9
	$150 000–$199 999	2	4.3
	More than $200 000	1	2.1

Note. Mean age = 59.1 ± 7.9 years; Mean # of child = 4.0 ± 3.7; Mean # of grandchild = 2.9 ± 1.3;
[a]Data were available from 43 participants.

alongside grandmothers. Grandmothers selected one grandchild they felt closest to if multiple grandchildren qualified. Thirty-one parents were biological children of the grandmothers. Grandmothers reported highly positive relationships with both parents (mothers: $M = 7.8 \pm 2.6$; fathers: $M = 7.5 \pm 3.1$) ($0 =$ poor and $10 =$ excellent).

Procedures

This study was approved by the Emory University Institutional Review Board. The pre-registered data collection protocol and raw data are available via the Open Science Framework (http://doi.org/10.17605/OSF.IO/6VXA4). Data analyses reported in this manuscript were not pre-registered.

Pre-experiment questionnaires

Once enrolled, participants accessed the online study portal to complete written informed consent and self-report questionnaires. Participants' involvement in instrumental caregiving was assessed with the Parental Responsibility Scale (PRS) (McBride and Mills, 1993). Financial support was measured as the proportion of income spent on grandchildren, and caregiving hours as weekly averages. Extent of supportive behaviors and positive feelings towards grandchildren were measured using the Supportive Engagement Behaviors (SEB) Index (Lovejoy et al., 1999) and the Positive Affect Index (PAI) (Bengtson and Schrader, 1982), modified to assess grandmaternal caregiving. Lastly, we collected indices on participants' mental and physical health that may influence their caregiving involvement, such as depression, loneliness, financial stress, and bodily pain **(SI-2, SI-3)**. The self-report questionnaires showed good internal consistency (Cronbach's alpha: 0.85–0.95) **(SI-2)**.

Main fMRI task

Participants were scanned with fMRI as they performed a face perception task (Fig. 1). Participants saw a series of photos depicting participants' OGC, an unknown grandchild (UGC), the same-sex parent of their grandchild (familiar parent, FP), an unknown adult parent (UP), and nonhuman objects (OBJ). Photos representing each category were shown 10 times in a predetermined sequence. Participants were instructed to observe the emotions shown in the stimuli if applicable. The duration of the main fMRI task was ~11 min.

Experimental stimuli

Before the fMRI experiment, the parents of the focal grandchild shared two front-facing, headshot photos of OGC and FP, with happy and neutral facial expressions. Extraneous visual elements were removed from the photos. The experimental stimuli used for UGC and UP were selected from photos submitted by other participants, matching the sex, age, and race of OGC and FP. A total of eight photos of OBJ were used as the experimental stimuli for OBJ.

Data acquisition and analysis

### Neuroimaging data acquisition

All neuroimaging data were acquired using a Siemens MAGNETOM Trio 3 T MRI scanner. Grandmothers lay in the scanner with a padded head restraint to minimize head movement. Each scanning session began with a localizer, followed by a T1-weighted MPRAGE anatomical scan with the following parameters: TR = 1.9 s, TE = 2.27 ms, matrix = 256 × 256, FOV = 250 mm, slice thickness = 1.00 mm, and gap = 0 mm. Following the anatomical scans, fMRI scans were acquired using an Echo Planar Imaging (EPI) sequence (TR = 1.2 s, TE = 30 ms, matrix = 74 × 74, FOV = 220 mm, slice thickness = 3.0 mm, and gap = 0 mm, 54 axial slices).

Neuroimaging data analysis

Neuroimaging data were processed and analyzed using the Functional Magnetic Resonance Imaging of the Brain's software library (FSL) (version 6.0).

Preprocessing

The preprocessing pipeline included motion correction (MCFLIRT), skull-stripping (BET), high-pass temporal filtering with
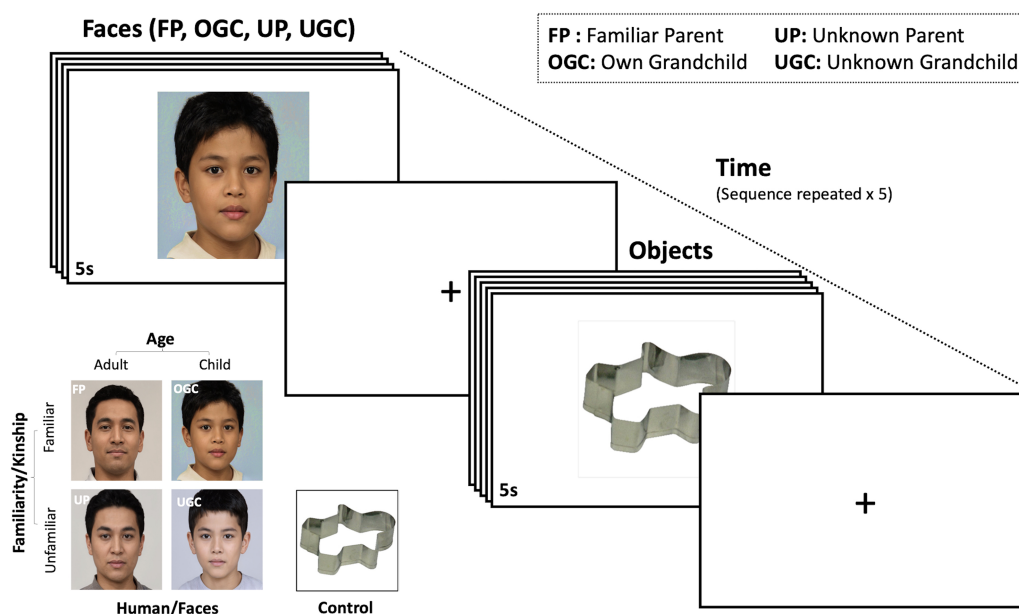
Figure 1. Schematic representation of the fMRI task. Participants were instructed to pay attention to stimuli and share the emotions of the targets, whenever applicable. AI-generated faces were used for creating the figure (https://generated.photos).

a cut-off of 100 s, and spatial smoothing with a Gaussian kernel of full-width at half maximum of 5 mm. Using FSL's linear registration tool (FLIRT), participants' functional- and high-resolution anatomical brain images were co-registered (Boundary-Based-Registration) and normalized to an MNI standard space (affine transformation). We also used a separate preprocessing pipeline without spatial smoothing and confirmed the robustness of the main RSA findings (**SI-8-2**).

Regions of Interest definition

We defined an *a priori* regions of interest (ROI) based on a meta-analytic association map generated from the search term "motivation" on NeuroSynth (FDR corrected $q < 0.01$) (https://neurosynth.org) (Motivation ROI) (Fig. 2a). To test the robustness of our main findings, we also created (i) a structural ROI mask spanning the same regions and (ii) an extended ROI mask including an additional brain region (i.e. the subgenual ACC) known to receive strong projections from the hypothalamic and striatal regions, supporting human bonding and social cognition (Öngür *et al.*, 1998; Atzil *et al.*, 2017; Lockwood and Wittmann, 2018). In addition, as described in the result section, we defined two *a posteriori* ROIs using the terms "Empathy" (Empathy ROI) and "theory of mind" (Mentalizing ROI). Additional details of *a posteriori* ROIs and anatomical ROI are provided in **SI-4** and **SI-8-1**.

Univariate analysis of the fMRI BOLD activation within the Motivation ROI

The univariate analysis had three objectives: (i) to generate input for RSA, (ii) to compare univariate vs. multivariate neural signatures of OGC and other social categories, and (iii) to examine their relationships with grandmaternal caregiving. The first-level general linear model (GLM) included five regressors for each stimulus category along with their temporal derivatives. Happy and neutral expressions were combined to increase trial numbers and stabilize parameter estimates; modeling these separately did not change the main results **(SI-10)**. Six motion parameters were included. Each explanatory variable (EV)'s time course was convolved with a double-gamma hemodynamic response function.

Beta weights for each stimulus category were estimated voxel-by-voxel and used in subsequent multivariate analyses. Single-trial modeling was avoided, as condition-wide modeling is generally more appropriate for tasks with repeated stimuli (Dimsdale-Zucker and Ranganath). For each participant, mean BOLD fMRI activations for each stimulus category within the Motivation ROI were extracted using *Featquery* and analyzed with repeated-measures ANOVA, followed by Bonferroni-corrected post-hoc tests for significant main effects.

Multivariate analysis of the activation pattern within the Motivation ROI

We performed an RSA using CoSMoMVPA (Oosterhof *et al.*, 2016) in MATLAB. For each participant, a dissimilarity index (1–Pearson's r) was computed between all pairs of stimulus categories, generating a 5×5 neural RDMs. The correlation distance was chosen for its sensitivity and invariance to differences in mean activation (Dimsdale-Zucker and Ranganath). Neural RDMs were processed with the DISTATIS algorithm in CoSMoMVPA, which calculates an optimal summary of the representational structure of the data in the form of a "compromise matrix" (Abdi *et al.*, 2005). The group-level compromise matrix was then submitted to multidimensional scaling and hierarchical clustering analyses in MATLAB via "midscale" and "linkage" functions in MATLAB.

We then evaluated the fit between neural RDMs from the Motivation ROI and model RDMs (see "'Model RDM Definition" section) using linear mixed-effects modeling (LMM) with random intercepts for participants and stimulus category pairs ("lme4") (Bates *et al.*, 2015). The likelihood-ratio test determined whether each model RDM significantly improved fit over the null model. Significant model RDMs were compared using Akaike Information Criteria (AIC) and marginal R^2. We also defined a separate LMM including all significant model RDMs and compared their fixed-effect estimates to further identify the best-fitting model.

Model RDM Definition

We constructed five model RDMs to identify the core organizing principles behind the multi-voxel neural representations of OGC
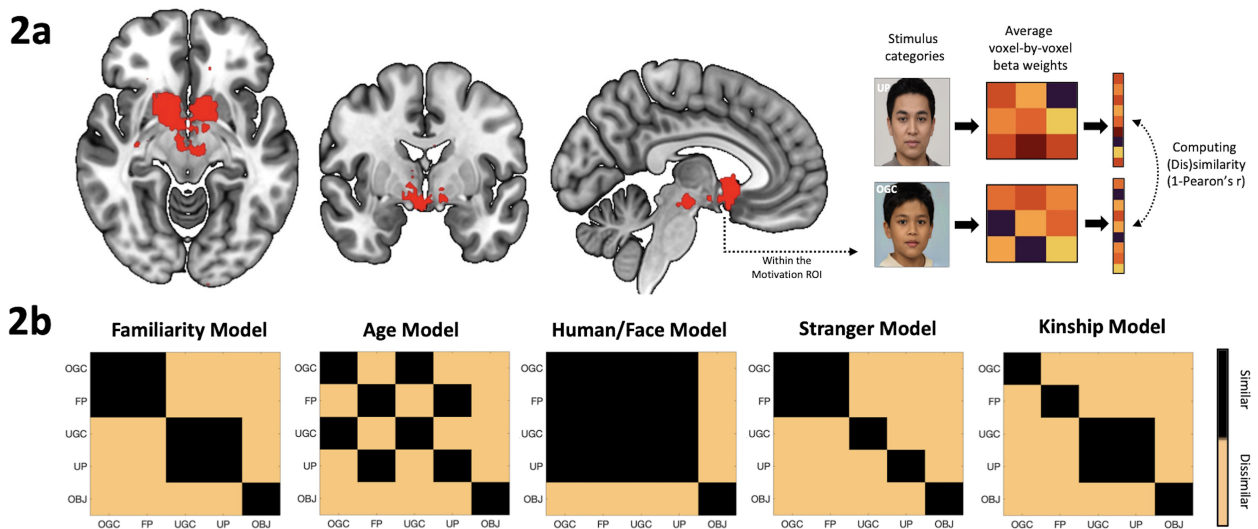
Figure 2. Motivation ROI mask and model RDMs. (a) The Motivation ROI mask was defined using a binarized meta-analytic association map derived from NeuroSynth (Search term: 'Motivation', FDR $q < 0.01$). The mask encompassed subregions in the striatum, hypothalamus, and midbrain, such as the NAcc, medial MPOA, and VTA/SN. A schematic representation of RSA is illustrated with UP and OGC as examples. (b) Five categorical model RDMs were created to capture theoretical representational structure sensitive to familiarity, human face, kinship, and strangers.

in the Motivation ROI (Fig. 2b): the "age" model clusters social categories based on infantile facial features; the "familiarity" model clusters social categories solely based on the shared experiences or knowledge; the "kinship" model, which aligns with our main predictions, assumes distinct representations for OGC and FP, while lumping non-kin; the "stranger" model sensitively distinguishes UGC and UP, while lumping kin; and the human/face separates all social-categories from OBJ. Additional descriptions and rationale for each of the five model RDMs are provided in **SI-11**.

Whole-brain searchlight RSA

We performed a whole-brain searchlight RSA to identify additional brain regions exhibiting a similar representational structure found in the Motivation ROI. The whole-brain association map derived from the best-fitting model RDM was contrasted with the average effects of other model RDMs. Details of our approach are provided in **SI-9**.

Analysis of self-report surveys and questionnaires

Participants' responses to the online self-report questionnaires were analyzed with SPSS (Version 29, IBM Corp., 2022) and R (Version 4.2.3, R Core Team, 2023).

Identifying dimensions of grandmaternal caregiving

To capture distinct dimensions of grandmaternal caregiving, we ran an exploratory factor analysis (EFA) using self-report questionnaire data. The EFA revealed two dimensions, namely, "Affective and Behavioral Support" and "Instrumental and Financial Support." The factor scores were calculated for each participant by applying the regression method and used for the correlation analyses described below. Details of the EFA procedures and results are summarized in **SI-5**.

Univariate vs. multivariate neural signatures of OGC in predicting grandmaternal caregiving

We performed correlation analyses with the neural dissimilarity measure for OGC extracted from the motivation ROI and the factor scores calculated for each participant. We used Spearman's ρ if the data were not normally distributed. We also repeated our analyses using the mean BOLD signals associated with OGC to examine whether the multivariate vs. univariate approach could reveal neural correlates of two grandmaternal caregiving dimensions.

All analyses on behavioral and questionnaire data were performed with the type-I error rate $\alpha = 0.05$ (two-tailed). The base significance threshold was adjusted for the total number of hypothesis-specific families of tests **(SI-1)**. The results of exploratory analyses were not corrected for multiple comparisons.

Results

Participants' background psychosocial characteristics and caregiving involvement

Our participants were generally healthy and had a stable economic standing. They also maintained highly positive relationships with focal grandchildren. Additional details of the self-report questionnaires are provided in **SI-3**.

Representation dissimilarity among the stimulus categories

The group-level compromise matrix and multidimensional scaling plot (Fig. 3a and b) revealed that UGC and UP were represented

similarly, while OGC and FP were more distinct. Hierarchical clustering (Fig. 3c) showed that OGC was uniquely separated from other social categories, indicating its high distinctiveness in neural representation. OBJ was the only category more distinct than OGC, clustering farthest from the social categories. Interestingly, FP clustered closer to UP and UGC than to OGC. Different distance measures (e.g. Euclidean and correlational distance) yielded the same clustering results.

### Comparison between the model RDMs and neural RDMs

Four of the five model RDMs showed significant associations with the neural RDM compared to the null model, with the Human/Face model rendered nonsignificant after multiple comparison corrections (adjusted $\alpha = 0.007$; Table 2). Consistent with **Prediction 1**, the kinship model explained the most variance and showed the best fit among all tested models. It remained the strongest predictor even when all significant model RDMs were compared in the same LMM **(SI-7)**. This result was robust to alternative ROI definitions, preprocessing methods, the inclusion of an additional model RDM accounting for emotional expressions **(SI-10)**, and grandchildren's age and grandmothers' living arrangement (e.g. co-residency status) **(SI-13)**.

Whole-brain searchlight RSA based on the kinship-sensitive model RDM

Our whole-brain searchlight RSA revealed additional brain areas outside the motivation ROI in which social and nonsocial categories are organized in accordance with the kinship model. Clusters of voxels showing significant nonzero correlations with the kinship model were identified in brain regions previously implicated in emotional empathy [e.g. dorsal anterior cingulate cortex (dACC), anterior insula (AI), and inferior frontal gyrus (IFG)], mentalizing [e.g. superior temporal sulcus (STS) and temporal pole (TP)] or reward and valuation [e.g. medial orbitofrontal gyrus (mOFC)] (Fig. 4, Table 3).

Neural distinctiveness of OGC in the Motivation ROI and grandmaternal caregiving

We examined whether the distinct multivariate neural signature of OGC in the Motivation ROI was associated with grandmaternal caregiving dimensions (adjusted $\alpha = 0.0125$). We calculated the average correlational distance between OGC and other social categories (OGC_{all}) and tested its associations with Supportive Affect and Behavior and Instrumental and Financial Support (adjusted $\alpha = 0.0125$). Two prior findings described above motivated this: the kinship model was the best-fitting model for the neural RDM, and OGC was the most distinct social category in hierarchical clustering (second only to OBJ). We also note that OGC showed the highest average pairwise dissimilarity among all social categories **(SI-6)**. Results showed a significant correlation between OGC_{all} and Supportive Affect and Behavior ($\rho = 0.392$, $P = .006$) but not Instrumental and Financial Support ($\rho = 0.144$, $P = .333$) (Fig. 5). Neither caregiving dimensions nor OGC_{all} was significantly associated with potential confounders, such as demographics, living arrangement (e.g. co-residence with OGC), mental and physical health, the number and age of children, the number and age of grandchildren, and years since transitioning into grandmotherhood (All P's > .075). Notably, the positive association between OGC_{all} and Supportive Affect and Behavior persisted ($B = 1.014$, $SE = 0.46$, $t = 2.188$, $P = .034$) after directly controlling for OGC's age and co-residency status, which are known to influence the
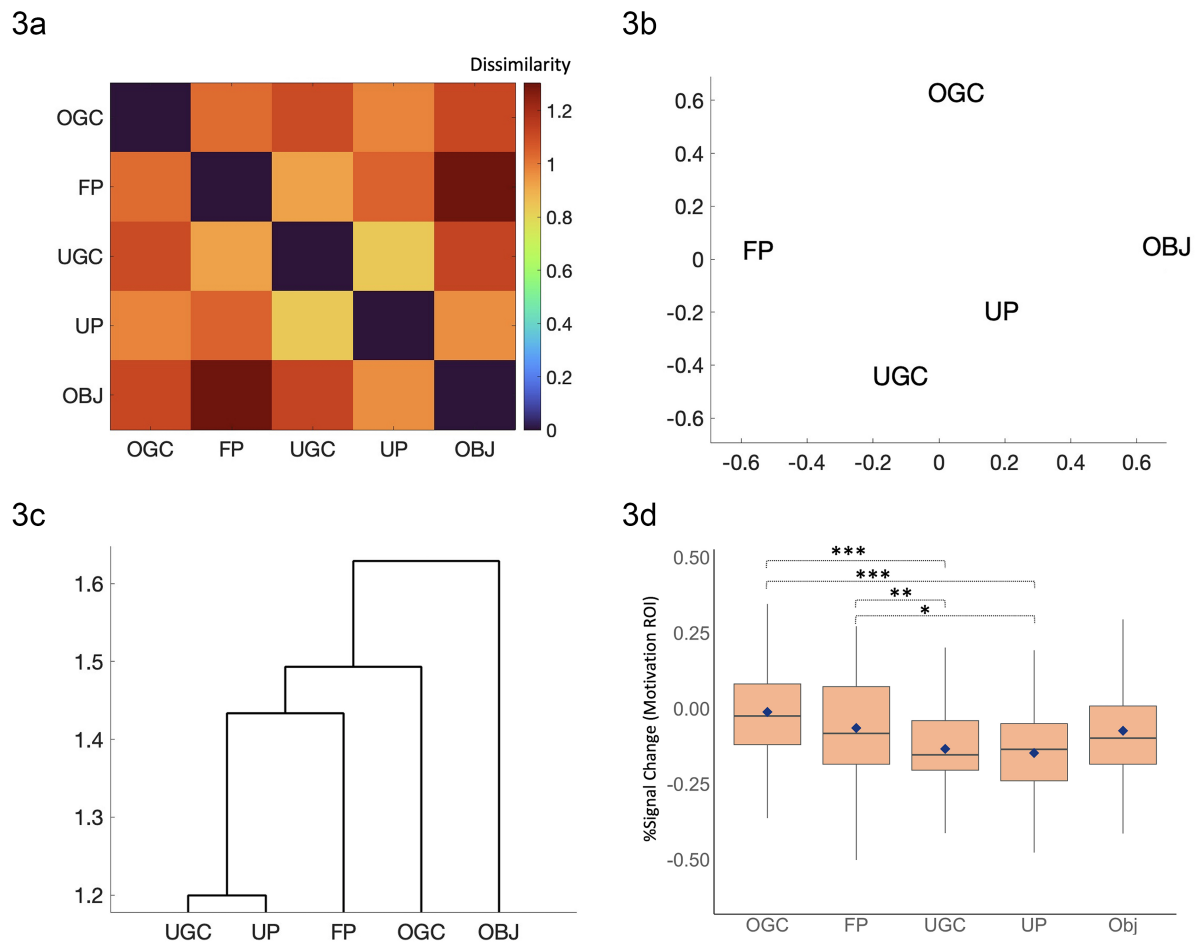
Figure 3. Representational structure of social and non-social categories in the Motivation ROI. (a) Neural RDM extracted from Motivation ROI. Different colours represent the pairwise correlation distance, with warmer colours representing greater dissimilarity. (b) Multidimensional scaling plot and (c) hierarchical clustering analysis showing the distinct multi-voxel neural representation of OGC. (d) Mean BOLD activation in the Motivation ROI associated with five stimulus categories.

Table 2. Summary of likelihood ratio test results against the null model

Model RDMs	Parameter estimates	SE	P	R^2_m	LRT χ^2	LL	AIC
Kinship model	0.82	0.09	<.001	0.44	33.7	−422.9	855.9
Stranger model	0.74	0.12	<.001	0.36	23.4	−428.1	866.1
Familiarity model	0.65	0.12	<.001	0.31	18.9	−430.3	870.6
Age model	0.55	0.14	<.001	0.23	12.0	−433.7	877.5
Human model	0.42	0.16	.013	0.13	6.1	−436.7	883.5
Null	-	-	-	0	-	−439.8	887.5

Note. Likelihood ratio tests (LRTs) were performed separately for each model RDM.

types and degrees of grandmothers' caregiving involvement (Pearson et al., 1997; Chapman et al., 2023; Aubel, 2024). FP was another distinct social category in the kinship model and showed high average dissimilarity values. But FP$_{all}$ did not correlate with any caregiving dimensions, demonstrating the specificity of the OGC effect (All *P*'s > .133).

Multivoxel neural representations of OGC in empathy and mentalizing ROI and grandmaternal caregiving

We explored whether the distinct multivoxel representation of OGC extracted from brain areas outside the Motivation ROI would also be associated with grandmaternal caregiving. We focused on the neural systems implicated in affective empathy and theory of mind, given their known roles in parental behaviors and altruism in humans (Swain et al., 2012). We calculated OGC$_{all}$ for two *a posteriori* ROI (Empathy ROI and Mentalizing ROI) and correlated the values with two caregiving dimensions (**SI-4**), finding no significant associations (All *P*'s > .374).

Mean fMRI BOLD response to the stimulus categories

Our repeated measure ANOVA model revealed a significant main effect of Category Type, $F_{(3.165, 142.4)} = 9.302$, $P < .001$, $\eta_p^2 = 0.17$ (Fig. 3d) (adjusted $\alpha = 0.007$). Post-hoc pairwise comparisons revealed that viewing the photos of OGC or FP elicited significantly greater neural activation than viewing the photos of UGC or UP (All *P*'s < .05). The average fMRI BOLD activations were not significantly different between OGC and FP or between UGC and UP (All corrected *P*'s > .726). Neural activities associated with OBJ were lower than OGC or FP and higher than UGC or UP,
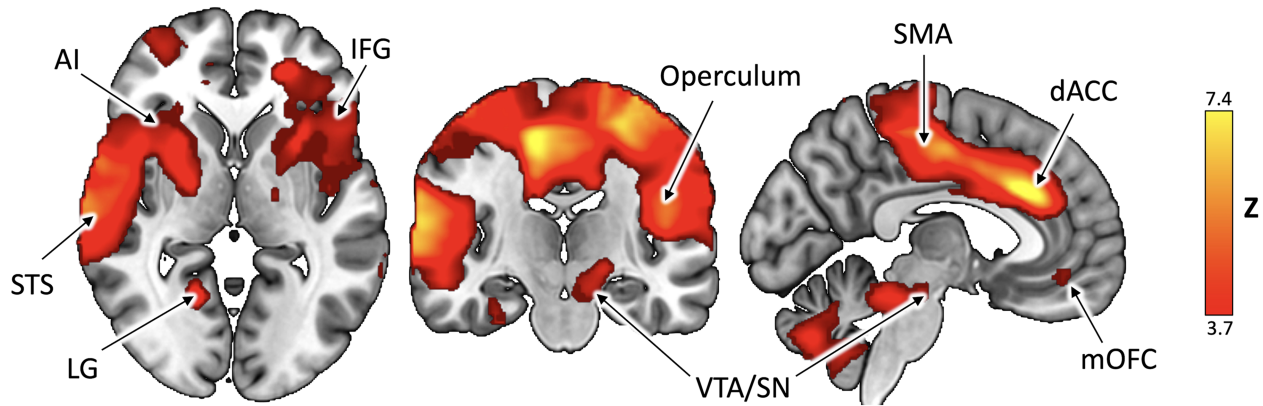
Figure 4. Whole-brain searchlight RSA. Outside regions originally included in the motivation ROI, a significant cluster was found in and around brain areas previously implicated in emotional empathy and mentalizing. Results are thresholded with cluster-level correction (Z > 3.7, cluster-level familywise error corrected P < .05) (AI = anterior insula, IFG = inferior frontal gyrus, STS = superior temporal sulcus, LG = lingual gyrus, VTA/SN = ventral tegmental area/substantia nigra, SMA = secondary motor area, dACC = dorsal anterior cingulate cortex, mOFC = medial orbitofrontal gyrus).

Table 3. Peak activation statistics for the results of whole-brain searchlight RSA

Anatomical regions	Hemi.	x	y	z	Z	K
Dorsal anterior cingulate cortex	L	−10	24	30	7.34	64 746
Lingual gyrus	R	18	−58	0	5.15	308
Medial orbitofrontal cortex	R	2	30	−18	4.05	6
Temporal pole	R	34	22	−40	3.84	5

Note. The clusters and peak voxels reflect the contrast [Kinship Model > (Familiarity + Age + Stranger Model)]. Only the clusters above $k > 5$ are reported.

although these differences did not reach statistical significance (All P's > .07). Overall, the univariate analysis yielded an activation pattern dissimilar to what was revealed by RSA.

Relationship between the average fMRI BOLD responses to OGC in Motivation ROI and grandmaternal caregiving

The average BOLD responses to OGC against implicit baseline did not significantly correlate with the two caregiving dimensions (adjusted $\alpha = 0.0125$) (All P's > .692). We also tested if the contrast estimates calculated between OGC and others [(OGC > FP), (OGC > UGC), (OGC > UP) and (OGC > GP + UGC + UP)] correlated with grandmaternal caregiving, finding no significant results (All P's > .189).

Effects of grandmothers' lineage and genetic relatedness to familiar parent

All grandmothers were biologically related to the focal grandchildren whose photos were used for the experiment. However, for 19 of the 47 participants, photos of a child-in-law were used in the fMRI experiment. This was intended to control for potential confounds related to OGC and FP having different genders. However, this may have influenced the neural representation of social categories in the Motivation ROI between grandmothers viewing photos of biological children vs. children-in-law. Additionally, 29 participants were maternal grandmothers. This is important as paternal grandmothers may show reduced caregiving investment due to uncertain paternity (Michalski and Shackelford, 2005). Factors like these could diminish the salience of OGC and alter its neural representation. Upon empirical examination, however, we

found no evidence that grouping grandmothers by their genetic relationship with FP (in-law vs. biological) or by lineage (paternal vs. maternal) affected our main univariate or multivariate fMRI results **(SI-12)**.

Lastly, we tested if the association between Supportive Affect and Behavior and OGC_{all} in the Motivation ROI differed between grandmothers who used in-laws (=Spousal grandmother) vs. biological children's photos (=Biological grandmother) for FP (GM_{SB}), or paternal vs. maternal grandmother (GM_{PM}). We defined two GLMs which included OGC_{all} and each of the two grouping variables as predictors and Supportive Affect and Behavior as a predicted variable. While no significant main effect nor interaction effects were found with GM_{SB} (All P's > .122), we found a significant main effect of GM_{PM}, OGC_{all}, and an interaction effect between $GM_{PM} * OGC_{all}$ (Table 4). Overall, maternal grandmothers reported higher Supportive Affect and Behavior than paternal grandmothers. Interestingly, OGC_{all} showed a stronger positive association ($\rho = 0.674$, $P = .001$) in paternal vs. maternal grandmothers (Fig. 6). This interaction effect persisted after controlling for the age of OGC, co-residency status, or work status of paternal vs. maternal grandmothers ($B = 5.385$, $F = 5.385$, $P = .015$).

Discussion

The present study investigated the neural mechanisms underlying grandmaternal caregiving by examining the representational structure of grandchild-related stimuli in the grandmother's brain. Using RSA, we found that grandchildren elicited patterns of neural activity distinct from other social categories in the neural systems previously implicated in mammalian parenting, most notably, mesolimbic and hypothalamic regions. This multi-voxel neural signature of grandchildren was further linked to individual differences in grandmaternal caregiving behaviors, specifically among paternal grandmothers.

Grandmothers' brains encode grandchildren as a distinct social category

Our key finding is that grandchildren were represented as a distinct category in the motivation ROI, second only to OBJ. This structure was best explained by the kinship model, where OGC and FP were separately represented, while no such sensitive distinction was made between UGC and UP. This pattern, robust across data preparation methods and ROI definitions, indicates
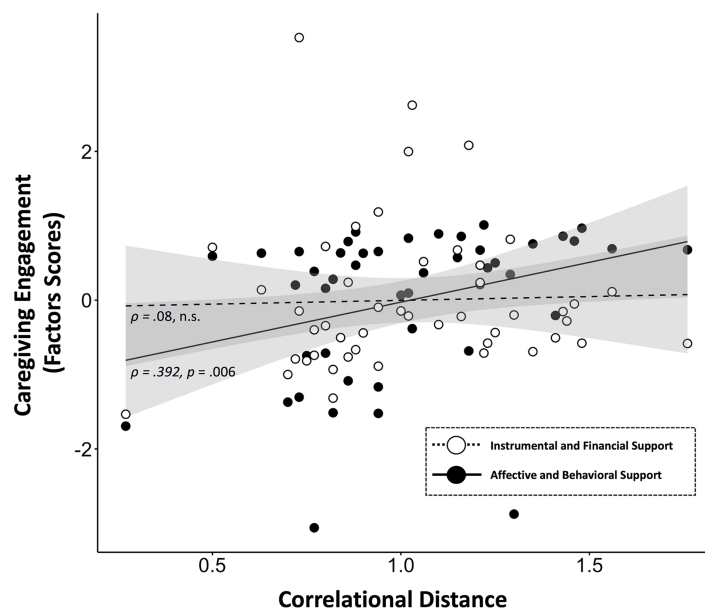
Figure 5. Distinct neural representation of OGC was associated with a specific dimension of grandmaternal caregiving. The average correlational distance between OGC and other social categories (FP, UGC, and UP) was positively associated (Spearman's ρ) with the Affective and Behavioral Support dimension of the grandmaternal caregiving but not Instrumental and Financial Support.

Table 4. The association between OGC_{all} and Supportive Affect and Behavior was modulated by grandmothers' lineage (Maternal vs. Paternal grandmothers)

Predictor	Type-III SS	B	df	MS	F	P	Partial η^2
(Intercept)	4.655	0.120	1	4.655	5.904	.019	0.121
GM Lineage	5.676	−2.54	1	5.676	7.198	.01	0.143
OGC_{all}	4.849	0.140	1	4.849	6.149	.017	0.236
GM lineage * OGC_{all}	3.713	0.196	1	3.713	4.709	.036	0.099
Error	14.17		36	0.789			

Note. The overall model was significant, $F = 5.113$, $P = .004$, $R^2 = 0.263$. GM Lineage = Paternal (dummy-coded: 0) vs. Maternal grandmothers (dummy-coded: 1), OGC_{all} = Average correlational distance calculated between grandchild and all social categories.

that the grandmaternal brain encodes kin, especially grandchildren, with heightened specificity, surpassing other organizing principles like age, familiarity, or emotion (Young *et al.*, 2017; Courtney and Meyer, 2020; Riberto *et al.*, 2022). According to the grandmother hypothesis, proximate mechanisms may help grandmothers invest in grandchildren (Scelza and Hinde, 2019). Prior research highlights the rewarding nature of alloparenting (Moore and Rosenthal, 2015). Our findings complement this psychological and narrative inquiry by showing that grandmothers' brains may encode grandchildren as a highly salient and unique category, which may serve as an important proximate mechanism of their engagement in caregiving at the neural level.

Distinct spatial representation of grandchildren in the Motivation ROI is associated with a subset of caregiving behaviors in grandmothers

Consistent with this interpretation, we found that grandmothers showing greater neural differentiation of their grandchildren—higher OGC_{all}—tended to show heightened affection towards grandchildren and engage in nurturing behaviors. This aligns with evidence linking hypothalamic and mesolimbic reward circuits to approach motivation and parental behaviors across species

(Rilling and Young, 2014). Here, the specificity of the association deserves a mention. That is, FP_{all}, despite showing similar neural distinctiveness as OGC_{all}, did not significantly correlate with any dimensions of grandmaternal caregiving. This null finding likely reflects the specificity of our caregiving measures, which focused on OGC rather than FP. Given that grandparents often provide financial and emotional support to their adult children and their spouses (Riem and van der Straaten, 2024), future research should examine whether distinct neural representations of FP relate to FP-directed affective or behavioral support.

Intriguingly, no significant association was found between OGC_{all} and Instrumental and Financial Support. This dimension of caregiving involves duties, time investment, and income allocation, which likely rely on cognitive processes besides the positive affect and caregiving motivation *per se*. For instance, executive functions, such as working memory or attentional capacity (Bhattacharyya *et al.*, 2024), are known to support a broad range of caregiving tasks, such as instrumental activity of daily living (IADL) assistance (Wang *et al.*, 2024). It is thus possible that neural activation in the prefrontal cortices (e.g. dorsolateral prefrontal cortex) (Wang *et al.*, 2022) may provide an additional window to grandmothers' capacity for or involvement of instrumental caregiving. Lastly, contextual factors, such as economic standing and proximity, may also influence instrumental caregiving, reducing the variance explained by neural processes in the Motivation ROIs.

Mean BOLD activation in the Motivation ROIs was not linked to grandmaternal caregiving

Consistent with previous works from our lab (Rilling *et al.*, 2021), we found increased mean BOLD signals in the Motivation ROI in response to OGC compared to other categories. Viewing the photos of FP also increased activation in the Motivation ROI. As FP was either grandmothers' biological children or their spouses, this activation suggests that the parental motivation circuits in the human brain are broadly engaged in maternal motivation—not just grandmaternal motivation—and are generally sensitive
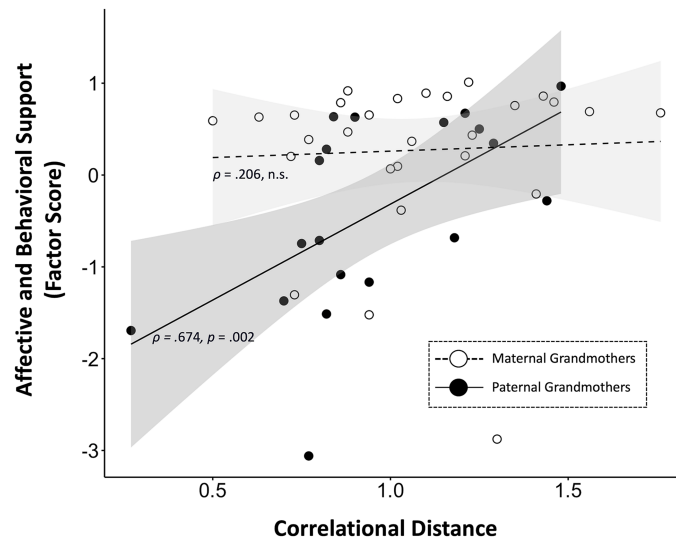
Figure 6. The association between the neural representation of OGC and grandmaternal caregiving was more pronounced among paternal grandmothers. Distinct multi-voxel representation of OGC was positively correlated with Affective and Behavioral Support stronger in paternal grandmothers than in maternal grandmothers, who generally engaged in greater caregiving, regardless of the distinct neural signatures of OGC.

to parenting-related cues. This echoes animal evidence implicating the hypothalamic (e.g. MPOA) and striatal subregions (e.g. NAcc) in parental motivation and alloparental care. Importantly, however, we found that the mean BOLD response to OGC did not show significant associations with any dimensions of grandmaternal caregiving. The diverging results from univariate and multivariate fMRI analyses in predicting grandmaternal caregiving recapitulate broader trends in social neuroscience, where multivariate methods often reveal unique neural processes that are obscured by averaging BOLD signals across voxels (Kriegeskorte and Bandettini, 2007). Our findings highlight RSA's sensitivity in identifying neural predictors of complex social behaviors, such as grandmaternal caregiving.

Distinct multivoxel neural representation of grandchild predicted caregiving more strongly among paternal vs. maternal grandmothers

The association between the multivoxel neural signature of OGC and caregiving behaviors raises questions about directionality: does caregiving experience shape OGC's distinct neural representation, or does this distinctiveness reflect a stable individual trait predicting caregiving? Our cross-sectional design limits direct testing of this question. However, exploratory analyses comparing maternal and paternal grandmothers provide insights. Maternal grandmothers engaged in Affective and Behavioral Support more than did paternal grandmothers, consistent with prior research (Pollet et al., 2007). Despite this difference, average OGC$_{all}$ and the explanatory power of the kinship model were similar between the two subgroups, suggesting caregiving experiences may not fully account for these neural patterns. The fact that OGC$_{all}$ did not significantly correlate with the total number of grandchildren nor with the lengths of grandmotherhood further corroborates the experience-independent nature of the relationship.

This leaves an intriguing alternative possibility where distinct neural representations of OGC in the Motivation ROI reflect a baseline preparedness or motivational readiness for caregiving across individuals that arises with grandmotherhood. This may explain why the association between OGC's neural patterns and caregiving behavior was stronger among paternal grandmothers,

despite similar levels of neural distinctiveness of OGC between maternal and paternal grandmothers. Evidence suggests caregiving is culturally prescribed as a "generational responsibility" (Mansilla-Domínguez et al., 2024), with such norms more salient for maternal grandmothers (Riem and van der Straaten, 2024). Maternal grandmothers, embedded in social structures encouraging caregiving, may engage in caregiving consistently regardless of their neural preparedness. In contrast, caregiving in paternal grandmothers, whose roles are less socially enforced, may be a more direct reflection of their motivational readiness as captured by OGC's neural representation.

Distinct multi-voxel neural representation of grandchild generalized to the putative caregiving network in the brain

Our whole-brain searchlight analysis identified additional brain regions that had similar representational structures to those in the Motivation ROI. These regions, implicated in emotional empathy and mentalizing, also showed increased BOLD responses to grandchild photos (Rilling et al., 2021). However, OGC$_{all}$ extracted from the Empathy and Mentalizing ROIs did not predict grandmaternal caregiving. While part of the caregiving network, these regions contribute to different aspects of parental behaviors (Rilling, 2013). Thus, such shared representational structures of OGC may not translate to the same psychological states or behaviors of grandmothers across these brain networks. Such heterogeneous representation-function correspondence was identified in previous fMRI studies employing multivariate approaches (Heinen et al., 2023. Future studies should elucidate the functions associated with the distinct neural encoding of OGC in the human caregiving network outside the Motivation ROI.

Limitations and future directions

This study has several limitations. While we tested the robustness of our findings across various data processing pipelines, the stability of OGC's multi-voxel neural representation requires further investigation. The limited stimuli and low repetition may reduce generalizability; future studies should include diverse stimuli, such as additional social categories (e.g. photos of relatives with

varying genetic distances from grandmothers) and modalities (e.g. written words vs. photos), to enable more rigorous validation of OGC's neural representation. Moreover, our sample may not adequately capture variations in caregiving norms across cultures, ethnic groups, and families (Aranda and Knight, 1997; Pharr *et al.*, 2014), which could influence both caregiving behaviors and their neural correlates. Including more diverse samples in future studies could enhance the generalizability of our findings. Longitudinal research are crucial to examine whether the distinct neural encoding of grandchildren and its relationship to caregiving behaviors are stable traits or dynamic, experience-dependent adaptations. If the neural encoding of OGC within the motivation ROI reflects preparedness for caregiving, it could be linked to psychosocial traits (e.g. empathy) or even lower-level biological mechanisms linked to caregiving. For example, recent studies found increased expression of the oxytocin receptor (*OXTR*) gene during late adulthood (Rokicki *et al.*, 2022) and potential decreases in *OXTR* DNA methylation following the transition to grandmotherhood (Rilling *et al.*, 2024). These changes may enhance caregiving motivation by upregulating *OXTR*-expressing neurons in the mesolimbic reward system, which may influence RSA results. Future research should explore these factors to better understand the neural representation of grandchildren in grandmothers' brains.

Conclusion

This study provides novel evidence that grandchildren elicit distinct neural representations in grandmothers, which predict caregiving behaviors. Despite limitations and its preliminary nature, our findings offer new insights into the neural mechanisms underlying grandmaternal caregiving, suggesting that motivational circuits encode grandchildren as a distinct category, potentially reflecting their adaptive and motivational significance. These results contribute to the broader mechanistic understanding of alloparenting and the grandmother hypothesis, while also highlighting the potential role of contextual factors that modulate the extent to which neural processes supporting caregiving motivations translate into actual caregiving behaviors.

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Author contributions

Minwoo Lee (Conceptualization, Formal analysis, Writing—original draft, Writing—review and editing); Amber Gonzalez (Data curation, review and editing); James K. Rilling (Writing—review and editing).

Supplementary data

Supplementary data is available at *SCAN* online.

Conflict of interest None declared.

Data availability

Data are available via OSF (http://doi.org/10.17605/OSF.IO/6VXA4).

References

Abdi, H, O'Toole, AJ, Valentin, D, Edelman, B. 'DISTATIS: the analysis of multiple distance matrices', 2005 *IEEE Computer Society Conference on Computer Vision and Pattern Recognition (CVPR'05)-Workshops* http://doi.org/10.1109/CVPR.2005.445, IEEE. 2005.

Aranda, MP, Knight, BG. The influence of ethnicity and culture on the caregiver stress and coping process: a sociocultural review and analysis. *Gerontologist* 1997;**37**:342–54. https://doi.org/10.1093/geront/37.3.342

Atzil, S, Touroutoglou, A, Rudy, T *et al.* Dopamine in the medial amygdala network mediates human bonding. *Proc Natl Acad Sci* 2017;**114**:2361–6. https://doi.org/10.1073/pnas.1612233114

Aubel, J. Grandmothers – a cultural resource for women and children's health and well-being across the life cycle. *Glob Health Promot* 2024;**31**:23–33. https://doi.org/10.1177/17579759231191494

Bartels, A, Zeki, S. The neural correlates of maternal and romantic love. *NeuroImage* 2004;**21**:1155–66. https://doi.org/10.1016/j.neuroimage.2003.11.003

Bates, D, Maechler, M, Bolker, B *et al.* Package 'lme4'. *Convergence* 2015;**12**:2.

Bengtson, VL, Schrader, SS. Parent-child relations. *Res Instrum Soc Gerontol* 1982;**2**:115–86.

Bhattacharyya, KK, Liu, Y, Das Gupta, D, Molinari, V, Fauth, EB. The healthy caregiver? A positive impact of informal caregiving status on cognitive functions over time from the midlife in the United States study. *J Aging Health* 2024;**36**:631–41. https://doi.org/10.1177/08982643231209482

Chapman, S, Danielsbacka, M, Tanskanen, AO, Lahdenperä, M, Pettay, J, Lummaa, V. Grandparental co-residence and grandchild survival: the role of resource competition in a pre-industrial population. *Behav Ecol* 2023;**34**:446–56. https://doi.org/10.1093/beheco/arad013

Chavez, RS, Heatherton, TF. Representational similarity of social and valence information in the medial pFC. *J Cogn Neurosci* 2015;**27**:73–82. https://doi.org/10.1162/jocn_a_00697

Connolly, AC, Guntupalli, JS, Gors, J *et al.* The representation of biological classes in the human brain. *J Neurosci* 2012;**32**:2608–18. https://doi.org/10.1523/JNEUROSCI.5547-11.2012

Courtney, AL, Meyer, ML. Self-other representation in the social brain reflects social connection. *J Neurosci* 2020;**40**:5616–27. https://doi.org/10.1523/JNEUROSCI.2826-19.2020

Dimsdale-Zucker, HR, Ranganath, C. Representational similarity analyses: a practical guide for functional MRI applications Manahan-Vaughan D. In: *Handbook of Behavioral Neuroscience*. Elsevier **28** (Handbook of in Vivo Neural Plasticity Techniques) 509-525 https://doi.org/10.1016/B978-0-12-812028-6.00027-6., 2018.

Hawkes, K, Coxworth, JE. Grandmothers and the evolution of human longevity: a review of findings and future directions. *Evol Anthropol: Issues News Rev* 2013;**22**:294–302. https://doi.org/10.1002/evan.21382

Hawkes, K, O'Connell, JF, Jones, NGB, Alvarez, H, Charnov, EL. Grandmothering, menopause, and the evolution of human life histories. *Proc Natl Acad Sci* 1998;**95**:1336–9. https://doi.org/10.1073/pnas.95.3.1336

Heinen, R, Bierbrauer, A, Wolf, OT, Axmacher, N. Representational formats of human memory traces. *Brain Struct Funct* 2024;**229**:513–29. https://doi.org/10.1007/s00429-023-02636-9

Hrdy, SB. Evolutionary context of human development: the cooperative breeding model. 2005.

Kramer, KL Cooperative breeding and its significance to the demographic success of humans. *Annu Rev Anthropol* 2010;**39**:417–36. https://doi.org/10.1146/annurev.anthro.012809.105054

Kriegeskorte, N, Bandettini, P. Analyzing for information, not activation, to exploit high-resolution fMRI. *NeuroImage* 2007;**38**:649–62. https://doi.org/10.1016/j.neuroimage.2007.02.022

Lee, AW, Brown, RE. Comparison of medial preoptic, amygdala, and nucleus accumbens lesions on parental behavior in California mice (Peromyscus californicus). *Physiol Behav* 2007;**92**:617–28. https://doi.org/10.1016/j.physbeh.2007.05.008

Lockwood, PL, Wittmann, MK. Ventral anterior cingulate cortex and social decision-making. *Neurosci Biobehav Rev* 2018;**92**:187–91. https://doi.org/10.1016/j.neubiorev.2018.05.030

Lovejoy, MC, Weis, R, O'Hare, E, Rubin, EC. Development and initial validation of the Parent Behavior Inventory. *Psychol Assess* 1999;**11**:534. https://doi.org/10.1037/1040-3590.11.4.534

Mansilla-Domínguez, JM, Recio-Vivas, AM, Lorenzo-Allegue, L, Cachón-Pérez, JM, Esteban-Gonzalo, L, Palacios-Ceña, D. The role of duty, gender and intergenerational care in grandmothers' parenting of grandchildren: a phenomenological qualitative study. *BMC Nurs* 2024;**23**:477. https://doi.org/10.1186/s12912-024-02151-0

Mascaro, JS, Hackett, PD, Rilling, JK. Differential neural responses to child and sexual stimuli in human fathers and non-fathers and their hormonal correlates. *Psychoneuroendocrinology* 2014;**46**:153–63. https://doi.org/10.1016/j.psyneuen.2014.04.014

McBride, BA, Mills, G. A comparison of mother and father involvement with their preschool age children. *Early Childhood Res Q* 1993;**8**:457–77. https://doi.org/10.1016/S0885-2006(05)80080-8

Michalski, RL, Shackelford, TK. Grandparental investment as a function of relational uncertainty and emotional closeness with parents. *Hum Nat* 2005;**16**:293–305. https://doi.org/10.1007/s12110-005-1012-5

Moore, SM, Rosenthal, DA. Personal growth, grandmother engagement and satisfaction among non-custodial grandmothers. *Aging Mental Health* 2015;**19**:136–43. https://doi.org/10.1080/13607863.2014.920302

Numan, M, Stolzenberg, DS. Medial preoptic area interactions with dopamine neural systems in the control of the onset and maintenance of maternal behavior in rats. *Front Neuroendocrinol* 2009;**30**:46–64. https://doi.org/10.1016/j.yfrne.2008.10.002

Olazabal, DE, Young, LJ. Oxytocin receptors in the nucleus accumbens facilitate "spontaneous" maternal behavior in adult female prairie voles. *Neuroscience* 2006;**141**:559–68. https://doi.org/10.1016/j.neuroscience.2006.04.017

Öngür, D, An, X, Price, J. Prefrontal cortical projections to the hypothalamus in macaque monkeys. *J Comp Neurol* 1998;**401**:480–505. https://doi.org/10.1002/(SICI)1096-9861(19981130)401:4<480::AID-CNE4>3.0.CO;2-F

Oosterhof, NN, Connolly, AC, Haxby, JV. CoSMoMVPA: multi-modal multivariate pattern analysis of neuroimaging data in Matlab/GNU Octave. *Front Neuroinformat* 2016;**10**:27. https://doi.org/10.3389/fninf.2016.00027

Pearson, JL, Hunter, AG, Cook, JM, Ialongo, NS, Kellam, SG. Grandmother involvement in child caregiving in an urban community. *Gerontologist* 1997;**37**:650–7. https://doi.org/10.1093/geront/37.5.650

Pharr, JR, Dodge Francis, C, Terry, C, Clark, MC. Culture, caregiving, and health: exploring the influence of culture on family caregiver experiences. *Int Sch Res Not* 2014;**2014**:689826.

Pollet, TV, Nettle, D, Nelissen, M. Maternal grandmothers do go the extra mile: factoring distance and lineage into differential contact with grandchildren. *Evol Psychol* 2007;**5**:147470490700500412. https://doi.org/10.1177/147470490700500412

Popal, H, Wang, Y, Olson, IR. A guide to representational similarity analysis for social neuroscience. *Soc Cogn Affect Neurosci* 2019;**14**:1243–53. https://doi.org/10.1093/scan/nsz099

Riberto, M, Paz, R, Pobric, G, Talmi, D. The neural representations of emotional experiences are more similar than those of neutral experiences. *J Neurosci* 2022;**42**:2772–85. https://doi.org/10.1523/JNEUROSCI.1490-21.2022

Riem, MM, van der Straaten, M. Grandmothers matter: how grandmothers promote maternal perinatal mental health and child development. *Front Psychol* 2024;**15**:1521335. https://doi.org/10.3389/fpsyg.2024.1521335

Rilling, JK. The neural and hormonal bases of human parental care. *Neuropsychologia* 2013;**51**:731–47. https://doi.org/10.1016/j.neuropsychologia.2012.12.017

Rilling, JK, Gonzalez, A, Lee, M. The neural correlates of grandmaternal caregiving. *Proc R Soc B* 2021;**288**:20211997. https://doi.org/10.1098/rspb.2021.1997

Rilling, JK, Lee, M, Zhou, C, Gonzalez, A, Lindo, J. Grandmotherhood is associated with reduced OXTR DNA methylation. *Psychoneuroendocrinology* 2024;**168**:107122. https://doi.org/10.1016/j.psyneuen.2024.107122

Rilling, JK, Young, LJ. The biology of mammalian parenting and its effect on offspring social development. *Science* 2014;**345**:771–6. https://doi.org/10.1126/science.1252723

Rokicki, J, Kaufmann, T, De Lange, A-MG *et al*. Oxytocin receptor expression patterns in the human brain across development. *Neuropsychopharmacology* **47** 8 2022:1550-1560 https://doi.org/10.1038/s41386-022-01305-5.

Scelza, BA, Hinde, K. Crucial contributions: a biocultural study of grandmothering during the perinatal period. *Hum Nat* 2019;**30**:371–97. https://doi.org/10.1007/s12110-019-09356-2

Stoeckel, LE, Palley, LS, Gollub, RL, Niemi, SM, Evins, AE, Pavlova, M. Patterns of brain activation when mothers view their own child and dog: an fMRI study. *PloS One* 2014;**9**:e107205. https://doi.org/10.1371/journal.pone.0107205

Strathearn, L, Fonagy, P, Amico, J, Montague, PR. Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropsychopharmacology* 2009;**34**:2655–66. https://doi.org/10.1038/npp.2009.103

Swain, JE, Kim, P, Spicer, J *et al*. Approaching the biology of human parental attachment: brain imaging, oxytocin and coordinated assessments of mothers and fathers. *Brain Res* 2014;**1580**:78–101. https://doi.org/10.1016/j.brainres.2014.03.007

Swain, JE, Konrath, S, Brown, SL *et al*. Parenting and beyond: common neurocircuits underlying parental and altruistic caregiving. *Parenting* 2012;**12**:115–23. https://doi.org/10.1080/15295192.2012.680409

Tsantani, M, Kriegeskorte, N, Storrs, K, Williams, AL, McGettigan, C, Garrido, L. FFA and OFA encode distinct types of face identity information. *J Neurosci* 2021;**41**:1952–69. https://doi.org/10.1523/JNEUROSCI.1449-20.2020

Wang, D, Rushton, S, Ledbetter, L, Graton, M, Ramos, K, Hendrix, CC. Factors associated with memory of informal caregivers: a scoping review protocol. *PloS One* 2024;**19**:e0295449. https://doi.org/10.1371/journal.pone.0295449

Wang, H-Y, Ren, L, Li, T *et al*. The impact of anxiety on the cognitive function of informal Parkinson's disease caregiver:

evidence from task-based and resting-state fNIRS. *Front Psychiatry* 2022;**13**:960953. https://doi.org/10.3389/fpsyt.2022.960953

Wu, Z, Autry, AE, Bergan, JF, Watabe-Uchida, M, Dulac, CG. Galanin neurons in the medial preoptic area govern parental behaviour. *Nature* 2014;**509**:325–30. https://doi.org/10.1038/nature13307

Young, KS, Parsons, CE, Stein, A, Vuust, P, Craske, MG, Kringelbach, ML. The neural basis of responsive caregiving behaviour: investigating temporal dynamics within the parental brain. *Behav Brain Res* 2017;**325**:105–16. https://doi.org/10.1016/j.bbr.2016.09.012