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Familial transmission of neural representations for mental arithmetic across two generations

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Parental skills are among the most powerful predictors of children's outcomes. While distal genetic and environmental pathways likely contribute to skill transmission within families, much less is known about the proximal neural markers that support the transmission of cognitive functioning from parents to children. It is also unclear whether brain similarity between parents and children predicts similarity in cognitive skills. In this study, we used fMRI to measure brain activity associated with mental arithmetic—a task for which intergenerational transmission is consistently observed—in 37 familial dyads of 8-y-old children and their mothers. Regardless of familial ties, multivariate searchlight representational similarity analyses revealed remarkable adult–child similarity in the neural representations of a signature of arithmetic processing, the problem-size effect, within a broad occipito-parieto-frontal system. Comparing familial to nonfamilial adult–child dyads, family-specific transmission of neural representations was identified in the bilateral anterior insula and left precentral gyrus, key regions of the arithmetic processing network. Mother–child neural similarity in the insula and precentral gyrus interacted with maternal skillto predict mother–child similarity in math and working memory skills, such that neural similarity was more positively related to behavioral similarity in dyads with lower-skilled than higher-skilled mothers. Therefore, increased parent–child neural similarity may particularly predict shared cognitive abilities among dyads where parents experience greater difficulties. Our findings demonstrate that task-related intergenerational neuroimaging can identify brain regions involved in the intergenerational transmission of cognitive skills. They may have relevance for identifying neural markers of learning disabilities through familial transmission.

intergenerational transmission | mental arithmetic | fMRI | brain similarity | representational searchlight similarity analyses

Significance

Parents strongly influence their children's cognitive development, but how these skills are transmitted through generations remains unclear. Using brain imaging, we examined whether there was resemblance in how the brains of mothers and their children support a cognitive skill for which intergenerational transmission is often observed, i.e., mental arithmetic. We found intergenerational neural similarity in the insula and precentral gyrus, brain areas typically associated with domain-general executive processing. Additionally, the relation between mother–child neural similarity in these regions and behavioral similarity in math and executive functioning varied depending on maternal skill level, being more positive for lower-skilled than higher-skilled mothers. Our findings may have relevance for identifying neural markers of learning disabilities through familial transmission.

Children resemble their parents in cognitive traits as much as in physical attributes, an observation supported by numerous studies showing that children's cognitive abilities often mirror those of their parents. Parent–child similarity in cognitive skill is observed both broadly (1, 2) and in specific domains such as executive functioning (3, 4), word reading (5, 6), and arithmetic (7, 8). Even foundational abilities, such as processing symbolic and nonsymbolic quantities, display familial similarity (7–9). Overall, parental cognitive functioning may be one of the strongest predictors of children's cognitive outcomes.

The distal mechanisms behind this familial transmission involve genetic factors (10, 11) as well as environmental influences, including parental attitudes, expectations, and home learning practices (12, 13). However, the more proximal neural markers mediating this transmission are less understood. A growing number of studies suggest that parents may transmit aspects of brain structure and function in regions associated with cognitive traits (14, 15). Brain similarity has also been linked to shared habits and emotional traits between parents and children (14, 15). For example, similarity in resting-state network connectivity correlates with parent–child resemblance in sleep routines, substance use, and emotional adjustment (16–18), although some of these relationships are moderated by family context (19). However, most intergenerational neuroimaging studies lack cognitive tasks or independent measures of cognitive traits. Therefore, it remains largely unknown whether the neural mechanisms underlying children's cognitive skills are more similar to those of their parents than to other adults. It is also unknown whether neurocognitive similarity between parents and children explains their skill resemblance.

The present study aimed to explore the family-specific transmission of neurocognitive functioning from parents to children, using mental arithmetic (i.e., solving arithmetic problems without reliance on external computational aids or physical notation systems)

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as a test case. We focused on mental arithmetic for two reasons. First, there are significant individual differences in arithmetic skills among children (20), and these individual differences are predicted by arithmetic abilities of parents (7, 8). Evidence for the familial transmission of arithmetic skills also comes from the observation that children with dyscalculia, a learning disability that affects arithmetic learning, are more likely to have a parent with the same condition (21). Second, mental arithmetic is a complex cognitive skill, involving both domain-specific representations of numerical quantities in the intraparietal sulcus (IPS) and domain-general executive functions in the prefrontal cortex (22). However, it remains unclear whether differences in domain-specific or domain-general mechanisms better explain variations in math skills (23), and notably dyscalculia (24). For example, while some studies suggest that math difficulties may relate to structural or functional differences in the IPS (25–33), others emphasize the role of the prefrontal cortex (25, 26, 28, 31, 34, 35). Investigating the transmission of neural mechanisms underlying mental arithmetic allows exploring whether similarity in cognitive skills between parents and children is due to neural similarity in the IPS or in prefrontal regions (or both), shedding light on the role of domain-specific versus domain-general mechanisms in mental arithmetic.

We recruited a sample of 60 familial dyads. Dyads consisted of mothers and their 8-y-old children. At this age, children begin transitioning from silent counting strategies during arithmetic problem solving to more efficient strategies (e.g., memory retrieval, automatized counting), making individual differences in arithmetic skills particularly apparent (36, 37). For example, dyscalculia may often begin to be identified around this age (38). Therefore, although most prior intergenerational neuroimaging studies have focused on adolescence and early adulthood (14), exploring family-specific mechanisms underlying arithmetic processing around age 8 may have clinical relevance for the identification of potential neuromarkers of learning difficulties. Here, math, working memory, and vocabulary skills of both children and mothers were assessed using psychometric tests to determine the extent of skill transmission within each dyad. We then used functional MRI (fMRI) to analyze brain activity related to mental arithmetic in a subsample of 37 familial dyads (Fig. 1). Using dyadic searchlight representational similarity analysis (RSA) across all possible adult–child pairs in the sample, we first identified brain regions showing intergenerational similarity in patterns of activity associated with increases in arithmetic problem size, a modulation that has been reliably associated with increases in response times (39) and brain activity (27, 37, 40–44) in both children and adults. Focusing on the problem size effect provides a particularly robust approach because it represents a parametric modulation of cognitive load that does not rely on potentially problematic assumptions about baseline conditions or arbitrary control tasks (45), making the manipulation well-adapted to comparison across age groups (37). We then compared familial and nonfamilial dyads to identify regions showing family-specific neural transmission. Finally, we investigated whether parent–child neural similarity predicted parent-child similarity in cognitive skills.

Results

Associations Between Cognitive Skills of Mothers and Cognitive Skills of Children. In the full sample of familial dyads (n = 60), we first tested whether cognitive skills measured through psychometric tests (i.e., math, working memory, and vocabulary) and response times to the arithmetic task performed in the scanner (Fig. 1*A*) were correlated between mothers and children.

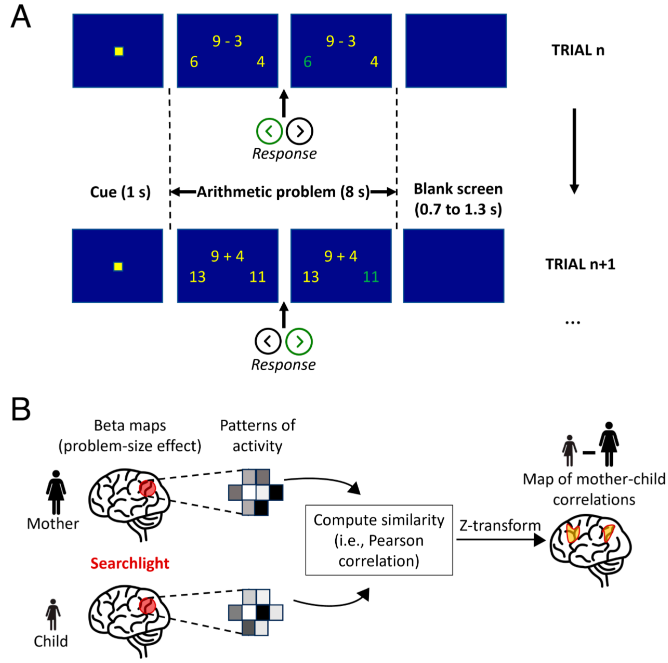

Fig. 1. Task and fMRI analysis strategy. (*A*) Example trials of the mental arithmetic task performed in the scanner. Each trial began with a 1-s cue, followed by an arithmetic problem presented with possible answers for 8 s. The selected response turned green. A blank screen of variable duration was displayed after each trial. (*B*) Dyadic multivariate fMRI analysis. After estimating whole-brain activity associated with increases in problem size for each participant in a dyad (mother and child) and for each operation (addition and subtraction), mother–child correlations between beta maps for problem size were computed using searchlight RSAs.

Fig. 2*A* shows the correlations between the raw scores of the psychometric tests conducted outside the scanner. Children's scores on their math assessment (Calculation subtest of the TEDI-MATH) were positively correlated with mothers' scores on the adult math assessment (Applied Problems subtest of the WJ-III) ($r(58) = 0.33$, $P = 0.009$) (Fig. 2*B*). Similarly, children's scores on their vocabulary test (NEMI-2) were positively correlated with mothers' scores on the adult vocabulary test (WAIS-IV) ($r(58) = 0.35$, $P = 0.006$). Finally, the correlation between mother–child scores on digit-span measures of working memory (NEMI-2 for children and WAIS-IV for mothers) also approached significance ($r(58) = 0.25$, $P = 0.06$). Therefore, cognitive skills in mothers were associated with similar skills in their children. Mother–child correlations were also relatively domain-specific, as we did not observe any significant correlations between different measures.

Although accuracy on the arithmetic task performed in the scanner was not correlated between mothers and children ($r(35) = 0.11$, $P = 0.52$), this was most likely because it was near-ceiling for mothers (average accuracy was 96% for mothers and 80% for children). In contrast, average response times (RTs) of children were positively correlated with RTs of mothers ($r(35) = 0.34$, $P = 0.04$), but this relation was significant only for addition problems (addition: $r(35) = 0.36$, $P = 0.03$; subtraction: $r(35) = 0.24$, $P = 0.15$) (Fig. 2*C*). For both addition and subtraction problems, RTs increased with problem size for both children (addition: $t(36) = 6.08$, $P < 0.001$; subtraction: $t(36) = 3.13$, $P = 0.003$) and mothers (addition: $t(36) = 10.82$, $P < 0.001$; subtraction: $t(36) = 5.80$, $P < 0.001$) (*SI Appendix*, Fig. S1). This indicates a robust problem size effect across all participants for both operations, consistent with previous studies (39). Although the slope of

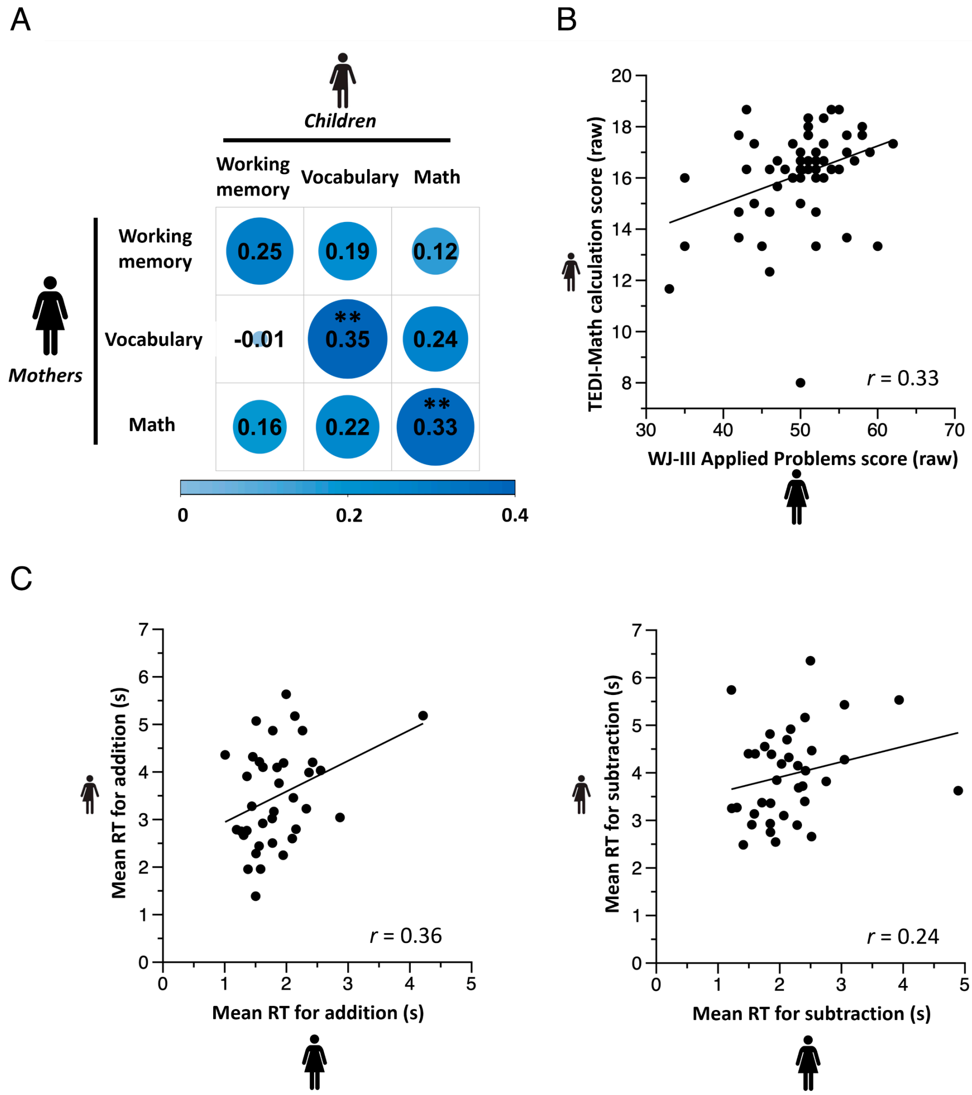

Fig. 2. Associations between cognitive skills of mothers and children. (*A*) Heatmap of Pearson correlations between raw scores of mothers and children shows significant within-domain mother–child associations for measures of math skills and vocabulary (*$P < 0.05$, **$P < 0.01$). (B) Raw scores of children on their math test (Calculation subtests of the TEDI-MATH) was positively related to raw scores of mothers on their math test (Applied Problems subtest of the WJ-III). (*C*) Average RTs of children on the mental arithmetic task was positively related to mothers' RTs for addition problems (*Left*), but the relation was not significant for subtraction problems (*Right*). Solid lines on the correlation plots indicate best-fitting regressions.

this problem size effect was not correlated between children and mothers (addition: $r(35) = 0.16$, $P = 0.36$; subtraction: $r(35) = 0.16$, $P = 0.35$), our behavioral results overall replicate the finding that children's skills are associated with their parents' skills.

Finally, we examined whether standardized math assessments collected outside of the scanner were related to performance in the arithmetic task performed in the scanner. The analyses revealed robust correlations between these measures. Children's scores on the Calculation subtest of the TEDI-MATH were positively related to in-scanner overall accuracy ($r(35) = 0.70$, $P < 0.001$) and negatively related to mean response time (addition: $r(35) = -0.57$, $P < 0.001$, subtraction: $r(35) = -0.55$, $P < 0.001$). Similarly, mothers' scores on the Applied Problems subtest of the WJ-III were positively related to overall accuracy ($r(35) = 0.53$, $P < 0.001$) and negatively related to mean response time (addition: $r(35) = -0.74$, $P < 0.001$, subtraction: $r(35) = -0.75$, $P < 0.001$). These findings demonstrate that performance on psychometric tests conducted outside the scanner provided a valid index of arithmetic performance in the scanner.

Intergenerational Similarity in Neural Responses Associated with Increases in Problem Size Across All Possible dyads. Before examining neural similarity between mothers and children using multivariate analyses, we first ensured that increases in addition and subtraction problem size were associated with univariate increases of activity across participants in IPS and prefrontal brain regions that have been identified in similar contrasts in prior studies (27, 37, 40, 41). After correction for multiple comparisons using voxel-level false discovery rate (FDR) correction, this was largely the case. Indeed, increases in activity associated with increases in problem size were found in several brain areas. These areas included the IPS, middle frontal gyrus (MFG), inferior frontal gyrus (IFG), as well as the middle occipital gyrus (MOG) for both adults and children and for both operations. Children also showed significant increases of activity in the bilateral insula for both operations (*SI Appendix*, Fig. S2).

Dyadic searchlight RSA (Fig. 1*B*) was then used to identify brain regions where patterns of activity associated with increases in problem size were similar across generations (maps were also FDR corrected at the voxel-level). This analysis was first conducted

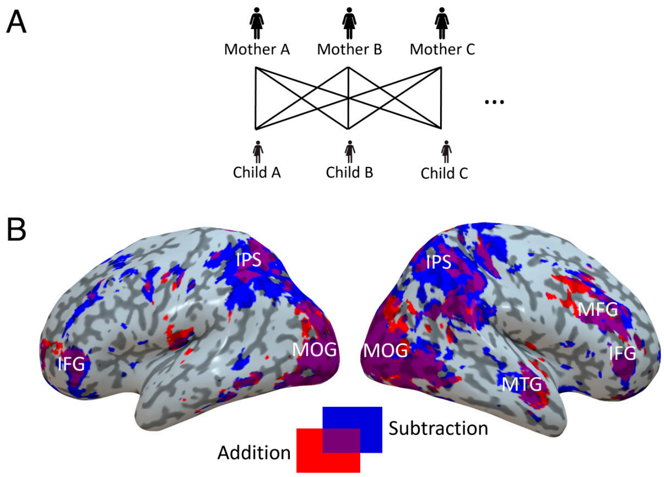

Fig. 3. Intergenerational similarity in neural responses associated with increases in arithmetic problem size across all possible dyads. (*A*) Schematic representation of the analysis strategy. Adult–child correlations between univariate beta maps of problem size (represented by solid lines) were calculated across all possible dyadic permutations within the entire sample. Overall neural similarity between generations was then computed across all possible adult–child dyads, separately for each operation. (*B*) Brain regions where patterns of activity associated with increases in addition (red) or subtraction (blue) problem size were similar across all possible dyads. Overlaps are shown in purple. Regions are overlaid on inflated renderings of the *Left* and *Right* hemispheres of an MNI-normalized brain. IPS: intraparietal sulcus, MOG: middle occipital gyrus, IFG: inferior frontal gyrus, MFG: middle frontal gyrus, MTG: middle temporal gyrus.

across all possible familial and nonfamilial adult–child dyads that could be generated from the entire sample of adults and children (n = 1,924 dyads) (Fig. 3*A*). Results are shown in Fig. 3*B* and *SI Appendix*, Table S1. For both operations (addition and subtraction), several brain areas showed significant pattern similarity between adults and children. Overlaps between similarity during mental addition and subtraction were notably observed in the bilateral IPS, MOG, IFG, as well as in the MFG and MTG. Thus, regardless of familial ties, representations of mental arithmetic were largely preserved across generations in a broad bilateral occipito-parieto-frontal system.

Family-Specific Intergenerational Similarity in Neural Responses Associated with Increases in Problem Size. To test how being from the same family influenced adult–child similarity in patterns of brain activity associated with the problem size effect, we identified the specific familial mother–child dyads from the entire set of adult–child dyads generated above. We then compared neural similarity in these familial dyads (n = 37) to neural similarity in all nonfamilial dyads (n = 1,887) to determine whether being from the same family increased adult–child similarity in specific brain regions (Fig. 4*A*). For addition, family-specific similarity in neural patterns associated with increases in arithmetic problem size was observed in three brain areas: the bilateral anterior insula (Left: x = −36, y = 16, z = 0, Z = 4.25, k = 28 voxels; Right: x = 34, y = 28, z = −2, Z = 8.92, k = 50 voxels) and the left precentral gyrus (x = −40, y = −2, z = 36, Z = 6.16, k = 27 voxels) (Fig. 4*B*). For subtraction, no cluster survived the FDR correction for multiple comparisons.

We then performed two control analyses to rule out alternative explanations of our findings. First, nonfamilial dyads in the above analysis included adults who were not part of the familial dyad group. To rule out the possibility that results might be confounded by differences in skills and traits between adults in familial and nonfamilial dyads (e.g., education, math ability, age), we repeated the analysis comparing neural similarity in familial dyads to neural similarity measured from nonfamilial dyads that were exclusively generated with participants included in the familial dyads (n = 1,332). Results were very similar to the main analysis reported above, with greater similarity in familial than nonfamilial dyads for addition in the left precentral gyrus and the anterior insula (though the cluster was only significant in the right hemisphere) (*SI Appendix*, Fig. S3).

Second, a characteristic of familial dyads is that children's skills are correlated with their mothers' skills. In other words, familial dyads exhibit some degree of behavioral similarity, both in cognitive skills and performance in the scanner (Fig. 2). Therefore, it remains unclear whether the increased neural similarity observed in these dyads is due to being from the same family or to having similar skills. To distinguish between these possibilities, we selected two control groups of 37 nonfamilial dyads each, matched to the group of 37 familial dyads in terms of similarity in math skills between adults and children. Therefore, correlations between the math skills of adults and children in these control groups were comparable to those observed in familial dyads (*SI Appendix*, Fig. S4). Critically, comparing these control groups to other nonfamilial dyads did not reveal any increase in similarity in either the bilateral anterior insula or the left precentral gyrus. This suggests that behavioral similarity between adults and children is not sufficient to increase neural similarity during mental addition in the left premotor cortex and bilateral anterior insula. Rather, the effect appears to be family specific.

Relations Between Neural Similarity and Behavioral Similarity. While the control analyses above indicate that neural similarity in the left precentral gyrus and the bilateral anterior insula reflects more than just behavioral similarity, it remains unclear whether neural similarity in these regions is actually related to behavioral similarity (i.e., the extent to which maternal skills are close to children's skills) across familial dyads. A critical consideration in interpreting any measure of behavioral similarity is that maternal skill should be taken into account. Indeed, behavioral similarity would be equally high when both mother and child are high-skilled but also when both mother and child are low-skilled, despite these cases reflecting qualitatively different scenarios. In other words, maternal skill can interact with (i.e., moderate) the relation between neural and behavioral similarity. Therefore, for each cognitive test (math, working memory, and vocabulary) and each brain region (left precentral gyrus, left anterior insula, right anterior insula), we conducted a moderation analysis using multiple regression with mother–child neural similarity (i.e., the Z-score representing the correlation between patterns for each dyad) as the predictor, mother–child behavioral similarity (calculated as 100 minus the absolute difference in percentile between mother and child for each dyad, such that higher scores indicate greater similarity) as the dependent variable, and mother's skill (i.e., maternal percentile) as the moderator.

Mother's skill showed no significant correlation with mother–child behavioral similarity across any cognitive domain (math: $r(35) = -0.05$, $P = 0.75$; working memory: $r(35) = -0.15$, $P = 0.36$; vocabulary: $r(35) = 0.22$, $P = 0.20$), confirming statistical independence between the moderator and dependent variable in all analyses. Main effects and interaction terms for each analysis are shown in *SI Appendix*, Table S2. Interaction terms were significant in two analyses.

The first analysis was a moderation model with neural similarity in the right anterior insula as the predictor, similarity in math scores as the dependent variable, and mother's math score as the moderator. Although neither the main effect of neural similarity nor the main effect of mother's math score was significant (neural

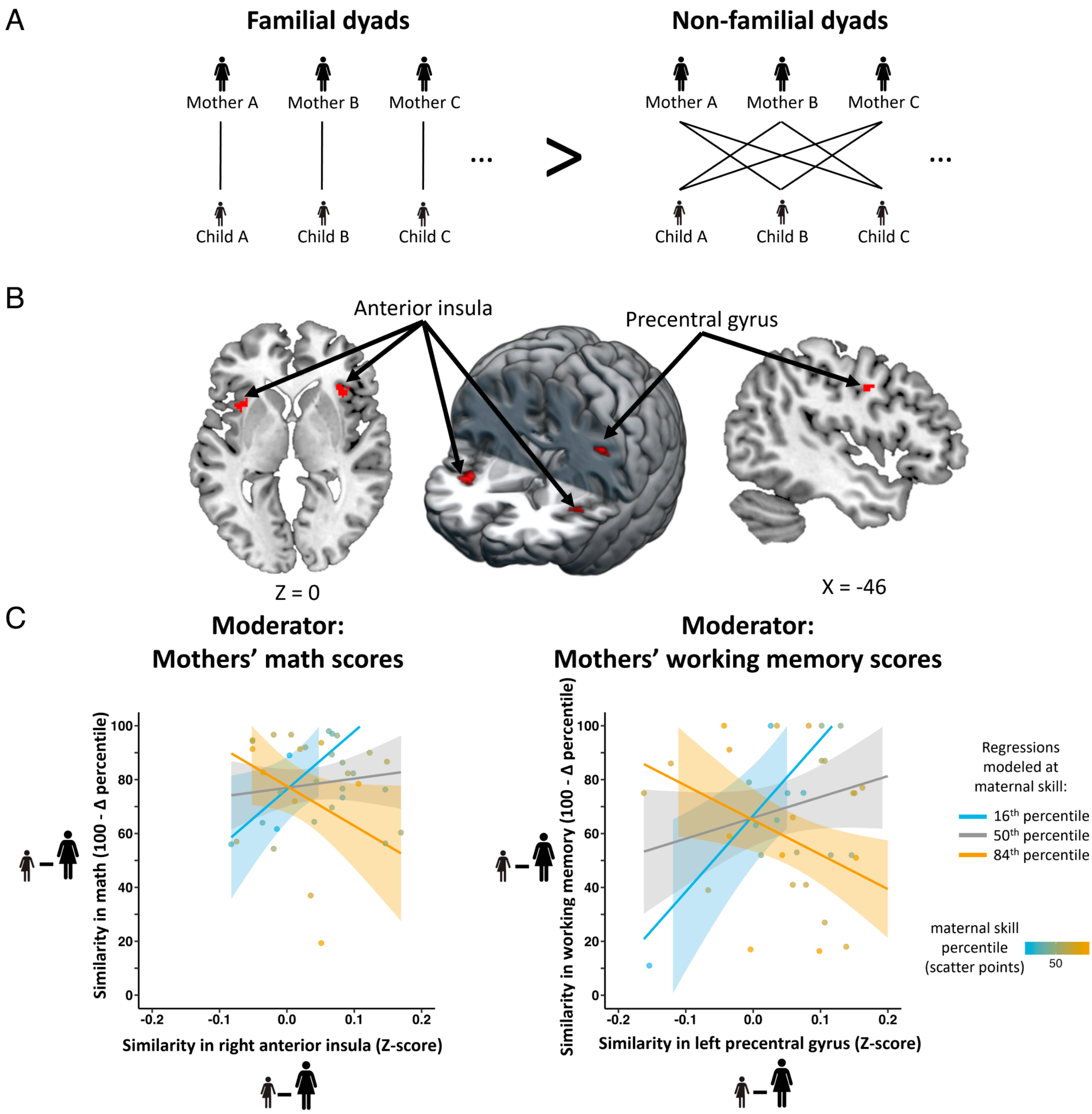

Fig. 4. Family-specific intergenerational similarity in neural responses associated with increases in arithmetic problem size. (*A*) Schematic representation of the analysis strategy. Family-specific neural similarity was measured by comparing adult–child correlations of activity patterns in familial dyads (*Left*) to those in nonfamilial dyads (*Right*), separately for each operation. (*B*) Brain regions where patterns of activity associated with increases in addition problem size were more similar in familial than in nonfamilial dyads, overlaid on a rendering and on axial and sagittal slices of an MNI-normalized brain. (*C*) Moderation analyses. The association between neural similarity and behavioral similarity depended on mothers' skills for the *Right* anterior insula and math scores (*Left*), as well as for the *Left* precentral gyrus and working memory scores (*Right*).

similarity: $\beta = 6.03$, SE = 41.41, $P = 0.88$; mother's math score: $\beta = -0.19$, SE = 0.12, $P = 0.09$), there was a significant interaction between mother's math score and neural similarity ($\beta = -5.33$, SE = 1.85, $P = 0.004$). This moderation indicated that mothers who had lower-than-average math scores exhibited a stronger positive association between neural similarity and similarity in math scores, when compared to mothers with average or higher-than-average math scores (Fig. 4 *C*, *Left*). Therefore, the association between neural similarity in the right anterior insula and similarity in math scores was significantly moderated by mother's math score.

The second significant interaction emerged from a moderation model examining neural similarity in the left precentral gyrus as the predictor, similarity in working memory scores as the dependent variable, and mother's working memory score as the moderator. Although there was no significant main effect of neural similarity ($\beta = -21.20$, SE = 40.70, $P = 0.60$), there was a significant main effect of mother's working memory score ($\beta = -0.37$, SE = 0.15, $P = 0.01$). Most importantly, there was a significant interaction between mother's working memory score and neural similarity ($\beta = -6.04$, SE = 1.45, $P < 0.001$), such that mothers with lower-than-average working memory scores exhibited a stronger positive association between neural similarity in the left precentral gyrus and similarity in working memory scores, when compared to mothers with average or higher-than-average working memory scores (Fig. 4 *C*, *Right*). Therefore, the association between neural similarity in the left precentral gyrus and working memory score similarity was significantly moderated by mothers' working memory score.

Although our main whole-brain analyses did not reveal family-specific similarity in neural patterns associated with increases in subtraction problem size (see above), for exploratory purposes, we also conducted moderation analyses on mother–child neural similarity associated with subtraction problems. We focused on the two associations identified for addition: i) the association between neural similarity and similarity in math scores in the right insula and ii) the association between neural similarity and similarity in working memory in the precentral gyrus. For subtraction, neither of these moderations was significant (right insula: $\beta = -0.90$, SE = 1.63, $P = 0.58$; precentral gyrus: $\beta = -2.18$, SE = 1.62, $P = 0.18$).

Discussion

Parental skills are strong predictors of children's cognitive outcomes. While distal genetic and environmental factors contribute, the proximal neuro-cognitive mechanisms underlying the transmission of cognitive skills from parents to children are less well understood. Using fMRI and dyadic searchlight RSA, we identified brain regions where parent–child representational similarity associated with increases in arithmetic problem size was greater in familial mother–child dyads compared to nonfamilial dyads. Regardless of familial ties, we found significant neural similarity across generations in several brain regions typically associated with math processing, including the IPS. However, family-specific neural similarity was only evident in three specific brain regions consistently involved in mental arithmetic across studies: the bilateral anterior insula and the left precentral gyrus. Intergenerational neural similarity in these regions interacted with mothers' skills to predict intergenerational behavioral similarity.

Symbolic arithmetic is a uniquely human cognitive skill whose intergenerational transmission is entirely cultural. It involves a large brain network that centers on the IPS (46, 47), a brain region critical to the domain-specific representation and manipulation of numerical quantities (48), but also encompasses regions supporting the visual and linguistic processing of arithmetic symbols in the occipital and inferior frontal cortices (22, 49) as well as domain-general mechanisms linked to working memory and attentional control in the prefrontal and anterior insular cortices (50). While there is extensive evidence that this large-scale brain system shows functional dynamics that vary considerably according to factors such as arithmetic operation (51–53), strategy use (54, 55), and development (22), it has also been argued that the system (particularly around the IPS) shows remarkable similarity in its neural architecture across cultures and individuals (56). This has motivated the "cultural recycling" hypothesis (56), according to which the human brain may represent symbolic arithmetic—a culturally acquired skill—by systematically recruiting evolutionarily conserved circuits. Our study extends this framework by demonstrating that this partial invariance in the neural architecture of arithmetic may be observed across generations, at the level of local activation patterns associated with increases in problem size in parietal, occipital, frontal, and temporal structures. This consistency in multivariate patterns across generations complements recent demonstrations of notation-independent arithmetic codes within individuals at the single-neuron level (57), suggesting that neural invariance for arithmetic processing operates across multiple scales of brain organization.

We identified family-specific transmission of neural representations in both the bilateral anterior insula and the left precentral gyrus. The anterior insula is one of the most consistently reported regions in functional neuroimaging studies of mental arithmetic (46, 50). Not only does activity in the anterior insula increase with arithmetic problem size in both adults and children (37), studies have also found unique associations between structural properties of the right anterior insular cortex and arithmetic skills (58). The specific role of the anterior insula in mental arithmetic remains unclear. However, as a key component of the salience network, the insula may help maintain focus on arithmetic problems by filtering out irrelevant stimuli and ensuring attention is directed toward different steps of mental computation (59, 60). Additionally, the role of the anterior insula in switching processing from default-mode regions to brain mechanisms that support attention and working memory (61) likely supports arithmetic calculation. Notably, this switching function may be fundamental to achieving the kind of efficient network engagement that has been recently proposed to underlie mathematical competence (23). Finally, the anterior insula may also support error monitoring by detecting mismatches between expected and actual outcomes (62), contributing to metacognitive awareness and error correction during arithmetic calculations (63). The idea that mother–child similarity in insular representations reflects similarity in attentional and monitoring mechanisms could explain the robust intergenerational correlations observed in measures of executive functions (4, 64).

The other region in which we observed family-specific neural similarity was the left precentral gyrus. Activation in the left precentral gyrus, particularly along the ventral and dorsal parts of the premotor cortex, is also frequently observed in neuroimaging studies of mental arithmetic (46). One interpretation is that the premotor cortex may support finger-counting strategies during arithmetic learning (65), potentially leading to long-term associations between mental arithmetic and finger representations in adults (66). Another interpretation, in keeping with our finding of a relation between intergenerational neural similarity in the left precentral gyrus and behavioral similarity in working memory (see below), is that the left precentral gyrus may support working memory (67). There is strong evidence that working memory is central to arithmetic processing (68). Therefore, the intergenerational neural similarity observed in the left precentral gyrus may reflect maternal influence on working memory processes in children.

Critically, mother–child neural similarity in the right insula and left precentral gyrus interacted with mother's skill to predict mother–child similarity in math and working memory scores (respectively), such that the relation between neural and behavioral similarity was more positive in dyads with lower-skilled mothers than in dyads with higher-skilled mothers. These findings suggest that neural patterns transmitted from mothers to children differently relate to the transmission of cognitive skills depending on the skill of the mother. Why would that relation depend on maternal skill level? One potential hypothesis is that the transmission of neural patterns might be more likely (or stronger) for lower-skilled than higher-skilled mothers. However, this hypothesis is unlikely because neural similarity in the right insula did not correlate with maternal math skill ($r(35) = 0.09$, $P = 0.60$), nor did neural similarity in the left precentral gyrus correlate with maternal working memory skill ($r(35) = 0.11$, $P = 0.52$). Therefore, neural patterns appear to be equally transmitted to children in these regions across all mothers.

An alternative and more plausible interpretation is that the mother–child transmission of neural patterns in the insula and precentral gyrus occurs to a similar extent across dyads with lower-skilled and higher-skilled mothers. However, this transmission is more likely to be positively associated with a closer behavioral similarity in lower-skilled mothers and their children than in higher-skilled mothers and their children. We speculate that this effect might stem from greater reliance on executive processing during mental arithmetic in both lower-skilled mothers and their children (compared to higher-skilled mothers and their children). Indeed, increased arithmetic proficiency is associated with both an expanded and more varied strategy repertoire as well as a decreased reliance on executive functions when implementing these strategies (69–71). This is notably suggested by studies that have investigated changes in brain activity following interventions aiming at improving arithmetic skills. In these studies, reduced use of inefficient strategies relying on executive control is often mirrored by reduced activity in prefrontal and insular regions (28, 72). Therefore, although neural patterns in these regions may be systematically transmitted from mother to child, this transmission may particularly influence performance when both mother and child employ similar and relatively inefficient strategies requiring greater executive demands (e.g., silent counting, decomposition). At age 8, children commonly rely on such strategies to varying degrees (36, 37), potentially more so in dyads with lower-scoring mothers (given the mother–child correlation in arithmetic performance). Mothers who scored lower on the standardized math assessment likely also employ these cognitively demanding strategies more frequently than higher-scoring mothers (as evidenced by longer response times and higher error rates during the arithmetic task in the scanner). If the transmission of neural patterns influences behavioral similarity through shared strategy use, then it is possible that children of higher-skilled mothers may also increasingly resemble their mothers as they become older and develop more efficient arithmetic skills, potentially in brain regions supporting retrieval-based (47) or automatized counting strategies (37). Future studies may test this prediction using concurrent strategy assessments during arithmetic problem-solving. Nonetheless, our findings suggest that examining neural pattern transmission in families where parents experience math difficulties may be a promising avenue for future studies aimed at identifying neuromarkers for developmental risk in children.

Are our findings of intergenerational neural similarity in the anterior insula and precentral gyrus generalizable to other related academic domains, such as reading? Although it is impossible to definitely answer this question with the current data, we note that there are striking similarities between the acquisition of arithmetic skills and learning to read, including the increase in strategy repertoire and a decrease in reliance on executive-demanding computational strategies (73, 74). Both the precentral gyrus and the anterior insula also contribute to reading fluency, for reasons that have also been attributed to executive functioning and error monitoring (75). Therefore, it is possible that our results might generalize to other high-level cognitive skills transmitted from parents to children, particularly where attention and performance monitoring are key (such as reading). However, even executive functioning may have some domain specificity (76), and intergenerational neural similarity in functional patterns may also depend on the cognitive task. This task-specificity is notably suggested by the fact that we found family-specific effects for addition but not subtraction problems. We speculate that this discrepancy arises from the greater heterogeneity of strategies associated with subtraction compared to addition, especially in children (77). This heterogeneity might have impacted our ability to detect family-specific neural similarity. It is possible that a larger sample size of familial dyads might have enabled us to detect family-specific neural similarity with subtraction, though we note that our sample is already larger than most previous neuroimaging studies focusing on parent–child transmission (19, 78–82). Still, our results with addition provide a proof of concept for the potential of dyadic searchlight RSA to detect the localization of neural similarity across parents and children in a task-related design.

Parents share both their genes and their environment with children, and both may lead to neural similarity. Therefore, similar to other intergenerational neuroimaging studies, it is unclear what proportion of environmental and genetic influences contribute to the family-specific brain markers that we identified (14). Disentangling these factors, which was not the goal of the study, would require genetically sensitive designs, such as genome-wide association studies. Nonetheless, it is interesting to note that twin studies have generally found relatively high heritability estimates for measures of brain structure (typically > 60%, though varying across regions and metrics) (83, 84), including for the anterior insula (85, 86). Studies show that measures of brain function are also under genetic influence, though heritability estimates tend to be lower (~40 % on average) and depend on the specific task, brain region, and analytical approach (84). For instance, using a pattern similarity methodology similar to the one used here, Etzel et al. (2020) (87) found that genetic factors may influence neural pattern similarity between individuals in regions supporting working-memory processing in the frontal cortex. However, studies also show significant environmental contributions to brain function, particularly during sensitive developmental periods, suggesting that environmental factors may also play a role in mediating brain network differentiation (83).

It is important to consider at least three potential methodological limitations of the present study. First, factors beyond the experimental manipulation might contribute to the observed neural pattern similarity. For example, the reliability of neural patterns in the prefrontal cortex is generally lower than in the visual cortex (70, 71 but see refs. 72 and 73). This consideration may be particularly relevant in our study given potential differences in neural signal reliability between children and adults. However, both the greater neural similarity in familial compared to nonfamilial dyads and the moderation of the relation between neural and behavioral similarity by maternal skill would be difficult to explain through reliability differences alone, as there is no obvious reason why pattern reliability would systematically vary in these cases. These aspects of our findings thus suggest that overall low pattern reliability is unlikely to explain our results.

Second, it is worth noting that our analysis pipeline required brains of both parents and children to be aligned to a common template, which in our case was a standard MNI template. It has been argued that normalizing developing brains into an adult template may introduce registration errors (88), which would have led to anatomical misalignments that may have limited our ability to detect regions of functional parent–child similarity. Nonetheless, it is worth noting that registration errors would have affected all adult–child dyads and therefore cannot explain the observed differences in similarities between familial and nonfamilial dyads. Still, future studies employing functional alignment procedures such as hyperalignment (89) might detect additional intergenerational similarities that might have been masked by anatomical misalignment in the current study.

Third, we examined neural pattern similarity associated with increases in the size of relatively simple arithmetic problems (e.g., single-digit addition), guided by the extensive literature investigating that effect at both behavioral (39) and neural levels (27, 37). Simple arithmetic problems (sometimes termed "arithmetic facts") are particularly valuable for investigation because they provide the foundation for more complex mental arithmetic and they can be solved by both adults and children with relatively high accuracy, enabling the examination of similarity in neural patterns (which would have been difficult with more complex problems). As stated in the Introduction, problem size has been associated with increases in both response times (39) and brain activity (27, 37, 40) in many studies, establishing these effects as hallmarks of arithmetic processing (39). Nonetheless, by definition, the neural problem size effect mirrors differences in behavioral performance levels. While this represents our effect of interest, this contrast may capture increases in cognitive load in a way that contrasting arithmetic problem solving to a performance-matched baseline would not. Although other contrasts used in the neuroimaging literature on arithmetic processing have largely converged on regions similar to those identified here (22) (*SI Appendix*, Fig. S2), differences in analytical approaches might affect mother–child neural similarity (potentially leading to less reliance on frontal regions if contrasts do not capture cognitive load).

In summary, the intergenerational transmission of skills from parents to children is one of the most robust observations in psychology. Focusing on a task for which intergenerational transmission is consistently observed—mental arithmetic—we demonstrate that this transmission is associated with family-specific similarity of neural representations associated with the problem size effect in the bilateral anterior insula and the left precentral gyrus. We further show that mother–child neural similarity in both the insula and precentral gyrus interacts with mother's skill to predict behavioral similarity in cognitive skills, with this relation being more positive among dyads with lower-skilled mothers. These regions have often been associated with domain-general executive processing. Therefore, these findings are consistent with and extend recent theoretical frameworks emphasizing the critical role of domain-general processes involved in network efficiency in mathematical cognition (23). By demonstrating that familial transmission of arithmetic processing manifests primarily in domain-general neural circuits, our findings lend some support for accounts suggesting that individual differences in arithmetic skills may reflect variations in executive functioning (90) rather than numerical processing per se (91). More generally, our results provide a proof of concept for detecting intergenerational neural similarity in brain activation patterns, which may contribute to future research on neural markers of skill transmission in learning disabilities that tend to run in families, such as dyslexia or dyscalculia (21, 92).

Material and Methods

Participants. A total of 119 individuals from 59 families were recruited for the study. The sample comprised 60 children, all 8 y old (mean age = 8.52, SD = 0.25, age range = 8.03-9.01; 31 females), along with their biological mothers. Due to the inclusion of a pair of twins, there were 59 mothers (mean age = 40.40, SD = 4.27, age range = 32.02 to 50.12). All participants were fluent French speakers residing in the Lyon area, France, and were contacted through advertisements on social media. Of the total sample, all participants were native French speakers with the exception of one mother whose native language was Arabic but who demonstrated fluency in French. Mothers provided written informed consent, and children gave their assent to participate. The study was approved by the local ethics committee (Comité pour la Protection des Personnes Est IV, n°2019-A01918-49). Children and mothers participated in two testing sessions on different days. The first session included standardized behavioral assessments for both mothers and children, as well as a familiarization with the MRI environment using a mock scanner for children. The second session involved fMRI testing. Families were compensated 60 euros for each testing session. Four dyads and two mothers did not participate in the second session. Nineteen children and one mother were excluded from the fMRI analyses due to i) discomfort in the scanner ($n = 1$ child), ii) technical issues ($n = 1$ child and $n = 1$ mother), and iii) excessive motion during the task ($n = 17$ children; see criteria below). Therefore, 37 children (mean age = 8.58, SD = 0.24, age range = 8.03 to 9.01; 24 females) and 52 mothers (mean age = 40.73, SD = 4.16, age range = 34.19 to 50.12) were included in the fMRI analyses, totaling 89 participants. Analyses of familial dyads only included the 37 mothers of the children who were not excluded (mean age = 41.47, SD = 4.15, age range = 34.19 to 50.12). Mothers reported their highest level of education in a questionnaire. Among all mothers included in the fMRI analyses, 11% reported having a vocational certificate or incomplete secondary education, 3% reported having only a secondary degree, 27% reported having an undergraduate degree, 51% a master's degree or higher, and 8% did not respond to the questionnaire. Therefore, the sample likely included families with a range of socioeconomic status (SES), though there was an overrepresentation of relatively high SES families. The anonymized behavioral data, individual beta maps, and analysis scripts are available on Zenodo (93).

Standardized Behavioral Assessment. Cognitive skills of both mothers and children were measured using several standardized tests. First, working memory was assessed using the digit span task. This task was taken from the Wechsler Adult Intelligence Scale-Fourth Edition (WAIS-IV) (94) for mothers and from the Nouvelle Echelle Métrique pour l'Intelligence 2 (NEMI-2) (95) for children. In this task, participants were given a series of digits that they had to repeat in the same order and in the reverse order (as well as in ascending order for mothers). The test began with two series of two digits and continued with series of increasing length until participants gave an incorrect response on two series of the same length. For each participant, we calculated a raw score representing the number of series repeated in the correct order (same, inverse, or ascending). Second, vocabulary was assessed using subtests of the WAIS-IV for mothers and the NEMI-2 for children. In these subtests, participants were given words to define. A raw score corresponding to the accuracy of each definition was obtained for each participant. Third, math abilities of dyads were assessed using age-appropriate tests that involved arithmetic processing. All mothers completed the Applied Problems subtest of the Woodcock-Johnson III Tests of Achievement (WJ III) (96), which assesses math problem-solving abilities through tasks that require mental arithmetic processing. While early items involve basic numerical operations (e.g., counting, mental addition and subtraction), later items present increasingly complex word problems requiring participants to maintain and manipulate multiple numerical elements mentally, without calculation aids. The untimed test continues until either six consecutive incorrect responses occur or the final item is completed, yielding a raw score reflecting the number of correct items. Although the Applied Problems subtest can be administered to children, available norms were collected only in the US population. While this limitation may not be problematic for adults given the consistency in math skills across two broadly comparable educational systems (97), it may substantially impact the validity of assessments in children due to potential differences in the timing of arithmetic acquisition within math curricula. Therefore, math skills of children were assessed with the Test Diagnostique des Compétences de Base en Mathématiques (TEDI-MATH) (98), which provides normative data for French children. Although the test assesses a range of math domains, we report here on the calculation subtest, which evaluates mental arithmetic through addition, subtraction, and multiplication operations, presented in both verbal and symbolic formats. A raw score was obtained for the subtest, reflecting the number of correct items. Finally, reading fluency was assessed for children only, using subtests from the EVALEO 6–15 (99). Participants had to read aloud two 450-word texts as quickly and accurately as possible within 2 min. One text was sensical, while the other was nonsensical. A reading score was calculated based on the average number of words correctly read for both texts. To help characterize the samples, all raw scores were transformed into standardized (i.e., age-normalized) scores. Percentile ranks corresponding to these standardized scores are presented in *SI Appendix*, Table S3. Mean scores across samples were in the average to high-average range, although there was a relatively large degree of variability in the performance of both adults and children.

Familiarization with the MRI Environment for Children. On the day of standardized testing, children were familiarized with the MRI environment using a mock scanner. They listened to a recording of the noises associated with all MRI sequences. A motion tracker system (3D Guidance TrackSTAR, Ascension Technology Corporation) was used to measure head movements and provide real-time feedback to participants. Finally, participants practiced 18 trials of the arithmetic task in the mock scanner. The arithmetic problems presented during the mock scanner session were different from those in the actual fMRI task.

fMRI Data Acquisition. Images were collected using a Siemens Prisma 3 T MRI scanner equipped with a 64-channel receiver head-neck coil (Siemens Healthcare, Erlangen, Germany) at the CERMEP Imagerie du vivant in Lyon, France. The fMRI blood oxygenation level-dependent (BOLD) signal was measured using a susceptibility-weighted single-shot echo planar imaging sequence. Imaging parameters were as follows: repetition time (TR) = 2,000 ms, echo time (TE) = 24 ms, flip angle = 80°, field of view (FOV) = 220 × 206 mm^2, resolution = 1.72 × 1.72 mm^2, slice thickness = 3 mm (0.48 mm gap), number of slices = 32. In addition to the functional scans, a high-resolution T1-weighted whole-brain anatomical volume was collected for each participant (TR = 2,400 ms, TE = 2.81 ms, flip angle = 8°, FOV = 224 × 256 mm^2, resolution = 1.0 × 1.0 mm^2, slice thickness = 1.0 mm, number of slices = 192).

fMRI Task. Participants were presented with a mental arithmetic task in the scanner (Fig. 1*A*). In each trial, an arithmetic problem was displayed on the screen along with two possible answers. Stimuli were presented in yellow on a blue background. Participants were asked to choose the correct answer as quickly and accurately as possible by pressing the corresponding response key. Each trial began with a 1-s cue consisting of a yellow square at the center of the screen. Each problem was then presented alongside two possible answers for 8 s. Selected answers were visually highlighted in green immediately upon selection, without providing feedback regarding response accuracy. The presentation of the problem was followed by a blank screen for 0.7 to 1.3 s. There were 32 trials, with 16 addition problems and 16 subtraction problems. All problems were presented in a fixed randomized order (see *SI Appendix*, Table S4 for a list of problems with their proposed answers). Incorrect answers were generated by either subtracting 1 (n = 8 trials) or 2 (n = 8 trials) from the correct answer, or by adding 1 (n = 8 trials) or 2 (n = 8 trials) to the correct answer. The task was coded and presented using PsychoPy software (100). A screen was installed at the end of the scanner bore, and stimuli were displayed by a projector in the room adjacent to the scanner. A 45° mirror was placed over the headrest so that participants could view the screen by looking upward. Head movement was minimized during the scan by cushions placed around the participant's head.

fMRI Data Quality Control. T1-weighted and fMRI images were converted to the BIDS (Brain Imaging Data Structure) format. The quality of the fMRI data was first assessed using MRIQC version 0.15.1 (101). The image quality metrics (IQMs) provided by the software were compared to an international database of quality metrics from the MRIQC web API, using the MRIQCeption tool. To define outliers, we used the following IQMs: AFNI's outlier ratio (aor), mean frame-wise displacement (fd_mean), intensity changes (DVARS_nstd), and global correlation (gcor). Data were considered outliers if at least one of these four IQMs was beyond a threshold defined by [median ± 2.5 × (75th percentile - 25th percentile)] compared with the API data. Out of the 106 participants who performed the arithmetic task (54 children and 52 mothers, forming 52 dyads), data from 17 dyads were excluded because the children (n = 17, including one of the twins) were classified as outliers for at least one of the IQMs.

fMRI Data Preprocessing. Data preprocessing was performed using fMRIPrep version 20.2.5 (102) with default parameters. fMRIPrep provides a standardized, robust preprocessing pipeline for fMRI data. Briefly, the pipeline included four main steps. First, fMRIPrep generated a reference volume and its skull-stripped version, which was used to estimate head motion using the mcflirt algorithm in FSL. Second, slice-timing correction was performed using the 3dTShift algorithm in AFNI (103), and time series were resampled in their native space. Third, functional images were coregistered to the anatomical image using the bbregister algorithm in FreeSurfer. Finally, using antsApplyTransforms (ANTs), images were normalized to the standard MNI152NLin2009cAsym template brain. Images were also resampled to obtain 2 mm isotropic voxels. No spatial smoothing was performed during preprocessing to preserve the spatial resolution of the images.

Individual Univariate fMRI Analysis. First-level individual analysis of fMRI data was performed using the Nilearn package in Python (104). Univariate activity associated with mental arithmetic was analyzed using a general linear model, where the fMRI signal for each arithmetic problem was modeled as an 8-s epoch starting with the presentation of the problem. Trials were sorted by operation (addition and subtraction). In addition to regressors coding for the average activity associated with addition and subtraction problems, the model also included the size of the problem as a parametric modulator for each operation. For addition, problem size was defined as the problem answer (i.e., the sum of the two operands), in line with several previous studies (37). For subtraction, studies have found that response time typically increases with both the problem answer (i.e., the difference between the first and second operand) and the size of the first operand (51). Therefore, problem size for subtraction problems was defined as the sum of the first operand and the problem answer. These two parametric regressors (one coding for the change in activity as addition problem size increases and the other for the change in activity as subtraction problem size increases) were considered the regressors of interest. Epochs were convolved with a canonical hemodynamic response function. Time series data from each run were high-pass filtered (1/100 Hz), and an ordinary least squares noise model was used for parameter estimation. Whole-brain beta maps corresponding to the parametric regressors of problem size were calculated for each operation and each participant. These maps were submitted to univariate t-tests across all participants (separately for children and mothers) to examine whether parametric contrasts of increases in problem size yielded clusters consistent with prior studies (27, 37, 40, 41).

Dyadic Multivariate fMRI Analysis. Similarity in the neural representations of mental arithmetic between adults and children was assessed using a searchlight RSA approach (Fig. 1*B*). Separately for each operation, we measured the adult–child correlation between univariate beta maps of problem size across all possible dyadic permutations within the entire sample (e.g., parent A correlated with child A, parent A correlated with child B, etc.) (Fig. 3*A*). This was done by calculating a Pearson correlation of the multivariate pattern of activity around each voxel of the brain using spherical searchlights with a 5-voxel (10-mm) radius (105). Pearson correlation coefficients were then converted to z-values using a Fisher transformation. The Fisher-transformed correlation coefficient for each searchlight was systematically associated with the central voxel of that searchlight. Thus, for each operation and possible dyad in the sample (n = 1,924, considering 37 children and 52 mothers), we obtained a z-map representing, at each voxel, the adult–child similarity (i.e., multivariate correlation) in the patterns of activity associated with an increase in problem size around that voxel.

Dyadic z-maps reflecting adult–child similarity in the problem size effect were then submitted to second-level testing. First, we evaluated neural similarity not specific to familiality using one-sample *t*-tests across all possible adult–child dyads (n = 1,924), separately for each operation. Second, we tested whether neural similarity was affected by familiality by comparing familial dyads (n = 37) (e.g., Adult A correlated with Child A, Adult B correlated with Child B, etc.) to all possible nonfamilial dyads (n = 1,887) (e.g., Adult A correlated with Child B, Adult B correlated with Child A, etc.) using two-sample t-tests, also separately for each operation (Fig. 4*A*).

Control analyses further tested whether the effects of familiality on neural similarity could be due to behavioral similarity between mothers and children rather than familiality itself. This was done by creating two groups of nonfamilial dyads matched to familial dyads in terms of sample size and degree of correlation between math skills of adults and children across dyads. The first group was created by ranking dyads based on children's percentile ranks on the TEDI-MATH and associating each mother with the child from the neighboring dyad (so that children were switched based on their similarity in math score). The second group was created by ranking dyads based on mothers' percentile ranks on the Applied Problems subtest of the WJ-III and associating each child with the mother from the neighboring dyad (so that mothers were switched based on their similarity in math score). We then tested whether neural similarity differed between these control groups of nonfamilial dyads (n = 37 in each group) and all other possible nonfamilial dyads (n = 1,850) using two-sample *t* tests, separately for each operation.

Whole-brain maps resulting from second-level analyses were z-transformed and corrected for multiple comparisons using a FDR correction at the voxel-level (106), which avoids potential issues with cluster-based corrections (107) while providing more power than voxel-level or even cluster-level familywise error rate (108). Voxel-level corrections may also be particularly suitable for searchlight analyses where the spatial extent of true effects may not match the assumptions underlying cluster-based corrections (105). Because our hypotheses are systematically directional (i.e., we are only testing whether neural similarity is greater than zero across all possible dyads and whether neural similarity is greater in familial than nonfamilial dyads), all maps were one-sided and the significance level was set at $P < 0.05$, one-tailed (voxel-level FDR-corrected, see above). To ensure robust interpretation of our findings, we applied two additional constraints. First, to ensure that observed differences between familial and nonfamilial dyads in FDR-corrected two-sample *t* tests arose from neural similarity in familial dyads rather than neural dissimilarity in nonfamilial dyads, only voxels where neural similarity in familial dyads was at least Z = 2.33 were visualized. The same procedure was applied in control analyses involving control groups of nonfamilial dyads. Second, even though voxel-level corrections allow for inferences at the level of single voxels (which represent individual searchlights in our case), only clusters of 10 voxels or more were visualized to enhance the interpretability and reliability of the results.

Moderation Analyses. To test whether the mother–child transmission of neural patterns was related to the transmission of skills from mothers to children, we conducted a series of moderation analyses in the brain regions identified in our main analyses (i.e., left precentral gyrus and the bilateral anterior insula). Specifically, we estimated the degree of mother–child behavioral similarity within each familial dyad by subtracting from 100 the absolute difference between the percentile ranks of children and mothers on their respective math, working memory, and vocabulary tests. This transformation yields a similarity score ranging from 0 (maximum dissimilarity) to 100 (perfect similarity). We also extracted neural similarity values for each dyad from the voxel showing the highest similarity across all familial dyads in the left precentral gyrus and the bilateral anterior insula for addition (i.e., the voxel representing the 10-mm radius searchlight in which the highest similarity was observed). The same coordinates were used to extract neural similarity values for each dyad for subtraction. For each brain region and operation, we then estimated: i) the relation between the predictor (i.e., the mother–child neural similarity) and the moderator (i.e., the skill of the mother); ii) the relation between the moderator and the dependent variable (i.e., the mother–child behavioral similarity), and iii) the interaction of the two relations above. The latter interaction term is the formal test of moderation (109). It indicates whether the relation between mother–child brain similarity and mother–child behavioral similarity increases or decreases with the skill of mothers.

Data, Materials, and Software Availability. The analysis scripts, anonymized behavioral data, and individual beta maps for each participant are available from Zenodo (https://doi.org/10.5281/zenodo.15098113) (93).

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