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ORIGINAL ARTICLE

Social Working Memory Predicts Social Network Size in Humans

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Abstract

Objectives The Social Brain Hypothesis posits a quantitative relationship between primate neocortex size and social network size. However, the precise social-cognitive mechanisms that drive this relationship remain elusive. Social Working Memory (SWM)—the ability to actively maintain and manipulate social information—has been proposed as a potential mechanism, but, to date, has not been linked to network size. Here, we explicitly tested this association.

Methods In Study 1, 125 participants completed a SWM task and reported on their social networks. In Study 2, 25 participants underwent fMRI during the SWM task and reported on their social networks.

Results As predicted, in Study 1, SWM performance was significantly associated with social network size and, specifically, "Sympathy Group" size (i.e., the size of one's core friend group). In Study 2, we conceptually replicated and extended this effect by showing that neural activity in the dorsal medial prefrontal cortex and medial prefrontal cortex engaged during SWM (vs. non-social working memory) was associated with individual variation in Sympathy Group size.

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Conclusions Taken together, these findings provide the first evidence that SWM constrains social network size, and suggest that SWM may be one social cognitive competency that underlies the Social Brain Hypothesis. In addition, whereas prior work investigating the Social Brain Hypothesis has largely focused on correlating brain structure size with social network size, to our knowledge, this is the first functional imaging evidence supporting the Social Brain Hypothesis.

Keywords Social working memory · Social networks · Social brain hypothesis · Neuroimaging · Evolution · Social bonds · Individual differences

According to the "Social Brain Hypothesis" (Dunbar 1998), the computational demands of living in complex and dynamic social groups selected for the relatively large brain-body size ratio that characterizes primates, including humans. Although originally proposed to explain species-level social and neural variation, much of the recent empirical work supporting the Social Brain Hypothesis has focused on individual variation in humans—for example, research indicates that prefrontal cortex gray matter volume predicts the number of people interacted with over a 1-month (Lewis et al. 2011), and 7-day period (Powell et al. 2010), and number of Facebook friends (Kanai et al. 2012).

A key proposition of Social Brain Hypothesis is that cortical volume constrains the number of social relationships that can be maintained by regulating information processing capacity (Dunbar 1992, 1993). To date, behavioural and neuroanatomical studies testing the Social Brain Hypothesis highlight the role of mentalizing (Lewis et al. 2011; Stiller and Dunbar 2007) in mediating the brain size-social network size association. However, mentalizing—an umbrella term used to describe thinking about people's mental states and personalities—is a broad construct and the precise mentalizing mechanism(s) at play are not fully understood. Social living requires keeping track of group members' characteristics and relative standing (e.g., who is generally more/less honest, anxious, enthusiastic, funny, etc.); thus, being able to reason about group members' traits may be a mentalizing process that is particularly important for developing and maintaining social networks. For example, being able to juggle such information would allow one to anticipate the needs and desires of others and, in this way, promote relationship well-being. Accordingly, we hypothesize that Social Working Memory (SWM; Meyer and Lieberman 2012; Meyer et al. 2012, 2015) may be one psychological mechanism that mediates the brain size-social network size association.

Of note, SWM overlaps with but is distinct from more general non-social working memory (non-SWM). Working memory has been defined as the active maintenance and manipulation of information in mind, without the aid of external environmental resources, such as pen and paper (Miyake and Shah 1999). Likewise, SWM is the active maintenance and manipulation of *social* information in mind, without support from external resources. While SWM involves more general working memory processes, functional imaging research indicates that SWM and non-SWM are at least partially functionally and anatomically distinct—specifically, SWM is supported by brain regions implicated in the canonical working memory system (i.e., lateral frontoparietal regions) as well as, critically, regions involved in mentalizing (i.e., medial frontoparietal regions; (Meyer et al. 2012). This finding is noteworthy because medial



frontoparietal regions typically show *decreased* activity during non-SWM tasks (see Gusnard et al. 2001). Moreover, subsequent research (Meyer et al. 2015) confirms that the medial frontoparietal system supports the social cognitive processes that increase with SWM load, whereas the lateral system supports the non-SWM operations that contribute to SWM task performance. That SWM uniquely increases activity in medial frontoparietal regions provides evidence that SWM is partially distinct from general non-SWM. Because SWM enables individuals to manage the social cognitive demands that accompany living in social networks, SWM is a good candidate mechanism for the Social Brain Hypothesis. It is not known, however, whether SWM predicts social network size—a key proposition of the Social Brain Hypothesis.

Here, we investigated the association between SWM and social network size in humans. Of note, social networks are conceptualized as hierarchically inclusive "circles" that capture different relationship kinds, with more central circles corresponding to greater emotional closeness and frequency of contact (Zhou et al. 2005; Dunbar 2014). For example, the "Sympathy Group", averaging 15 people, consists of core friends who provide "higher-cost" support (e.g., help with a move) and with whom one maintains regular contact (Dunbar and Spoors 1995), whereas the "Active Network", typically around 150 people, consists of weaker-tie relationships that provide "low cost" support, and with whom contact is more irregular (Dunbar 1992; Hill and Dunbar 2003). Because people typically spend more time navigating Sympathy Group (vs., e.g., Active Network) relationships (Dunbar 2014), and because misunderstandings occurring in those relationships should entail greater costs for the individual and the relationship (due to their greater emotional closeness), we hypothesized that SWM should be most strongly predictive of Sympathy Group size.

This hypothesis was tested in two studies. In Study 1, participants completed a task measuring SWM and reported on their social networks. In Study 2, we aimed to conceptually replicate and extend our understanding of this effect by investigating whether brain activity engaged during SWM similarly predicts Sympathy Group size. Of note, prior imaging work supporting the Social Brain Hypothesis has focused primarily on linking brain *structure* size with social network size. To our knowledge, no one has linked functional imaging correlates of social cognitive task performance with social network size. We believe this is a critical missing link given that the association between brain structure and network size should be mediated by social information processing ability.

Study 1

Methods

We recruited 140 participants from the McGill University community during the Fall and Winter academic terms. Participants received either course credit or \$10/h. in compensation. All participants provided written informed consent and the study was conducted in accordance with local Institutional Review Board guidelines. Fifteen participants were excluded from analyses because of: technical problems (n = 4), failure to comply with instructions (n = 3), or incomplete data on the Social Network Score Questionnaire (n = 8). Thus, the final sample consisted of 125 participants; there were 43 males and 81 females (1 whose gender was unreported); mean age was 20.64



 ± 2.35 years. Analyses indicate that our sample has the power to detect a medium effect at p < .05 with 90% power.

Of note, this study was originally an undergraduate honour's thesis. Results from the 64 participants comprising that thesis supported our hypothesis that SWM is associated with Sympathy Group size. Based on these preliminary results, we pre-registered (https://osf.io/7jw5b/) our intention to recruit additional participants and to pool the data to bolster the sample size of this small study. Other than the initial data analyses that were conducted for the honour's thesis, no other data analyses were conducted before data collection was complete.

Procedure and Measures

Participants first completed an on-line questionnaire to generate stimuli for the SWM task. Approximately 2 weeks later, they came to the lab and completed the Social Network Score Questionnaire followed by the SWM task about 10 min later. Participants also completed other questionnaires and tasks unrelated to the current hypothesis.

Social Working Memory Task (Meyer et al. 2012, 2015) This is a computer-based task designed to assess people's ability to maintain and manipulate varying amounts of social information. Approximately 2 weeks prior to the lab session, participants complete an on-line questionnaire in which they rank 10 friends on various traits using a 1–100 scale; these rankings are then used to generate individually tailored stimuli for the SWM task. The SWM task itself consists of 18 SWM trials in which participants are randomly presented with two, three, or four friends' names. Participants are then presented with one of the traits assessed 2 weeks prior (e.g., "enthusiastic") and are instructed to mentally rank the friends along that trait dimension. Following this mental ranking, participants answer a true/false probe about their ranking ("First? Jane"). In addition to the 18 SWM trials, there are 18 control trials during which participants are instructed to alphabetize two, three, or four of their friends' names. These trials were originally developed for a functional imaging protocol to tap more general non-SWM processes so that neural activity specifically associated with *social* working memory can be isolated.

Social Network Score Questionnaire (SNSQ) The SNSQ is a 9-item open-response questionnaire measuring the size of people's real-world social networks. Although the

² Of note, additional data from another sample of 56 participants who completed the SWM paradigm on two occasions, 12 days apart, indicate that the task is reliable (Meyer & Lieberman, unpublished data). Specifically, the Time 1 and Time 2 correlation for SWM (r(54) = .40) and non-SWM (r(54) = .42) were significant (both p's < .003), and were not significantly different from one another (p = .91), suggesting that they are similarly reliable.



¹ As indicated in our pre-registration, we aimed to recruit an additional 100 participants. In an effort to expedite data collection, we deviated from our original procedures and recruited some participants over the summer months (May–August), relying solely on on-line classified ads. These participants (N = 24), however, differed, significantly, from those recruited during the academic terms (N = 140); they were older (t (154) = -4.46, p < 0.001), more educated (t (155) = -4.59, p < 0.001), more likely to be employed full-time ($\chi = 22.31$, p < 0.001), and less likely to be in school ($\chi = 10.28$, p < 0.001), and, perhaps most importantly, performed significantly better on the SWM task (t (154) = -2.24, t = 0.027). Because of the different recruitment procedures and because they differed in non-trivial ways from the main sample, we excluded them from the analyses.

SNSQ is described as measuring a single construct (Kanai et al. 2012), we hypothesized that the SNSQ items capture different facets of the social network. Specifically, theory and research indicate that people's social network consists of qualitatively different social relationships that vary in emotional closeness and frequency of contact (Dunbar 2014), and inspection of the SNSQ items suggest that they tap these different kinds (e.g., "How many friends do you have on 'Facebook'?" vs. "Write down the names of the people of whom you feel you could ask a favour and expect to have it granted."). Consistent with this reasoning, analyses revealed that the SNSO showed poor internal reliability ($\alpha = 0.44$). We thus conducted a principal components analysis (PCA) with direct oblimin rotation on the SNSO items to determine whether a multiple component solution fit the data better. Before conducting the PCA we winsorized outliers that were more than three standard deviations from the mean to be one unit larger than the next most extreme score in the distribution (Tabachnick and Fidell 2007), and we applied a square root transformation to each SNSQ item to correct for skewness (>2.1 for each item), as other studies have done (Kanai et al. 2012). These pre-processing steps were taken because the PCA requires normally distributed data.

The PCA revealed three components with eigenvalues over Kaiser's criterion of 1, which, in combination, explained 59.5% of the variance (see Table S1 for complete descriptive statistics and a summary of principal components analysis results). An examination of the scree plot supported a three-component interpretation. The first component reflected Dunbar's Sympathy Group (eigenvalue = 2.77), or core friends with whom one maintains regular contact (median = 13, mean = 18 ± 16). The second component reflected Dunbar's Active Network (eigenvalue = 1.33), or one's extended social network (median = 205, mean = 254 ± 178). Notably, supporting our interpretation, descriptive statistics are consistent with theoretical predictions about the relative size of the Sympathy Group and Active Network. The third unexpected component appeared to reflect friends with whom one celebrates special occasions; for this reason, we coined this group the "Celebration Group" (eigenvalue = 1.25). Because the Celebration Group was unexpected, and because it did not readily map onto prior theorizing about social networks (e.g., as depicted in Fig. 1), we did not include this group in our primary analyses, but it is worth noting that additional analyses showed no association between SWM and Celebration Group size (the interested reader is referred to the Supplementary Materials for details and interpretation of the Celebration Group).

Results

To test our hypothesis, we investigated the correlation between SWM and the Sympathy Group and Active Network components separately (using the estimated component scores generated by the PCA).³ As expected, SWM performance significantly predicted Sympathy Group size, such that those individuals who had superior SWM reported more people with whom they could, for instance, count on for a favour, r(123) = 0.18, p = 0.046. SWM, however, was not significantly related to Active Network size, r(123) = 0.08, p > 0.250, suggesting that SWM is uniquely predictive of Sympathy Group size.

 $[\]overline{^3}$ For the interested reader, we examined the effect of gender on SWM, non-social working memory, and both network sizes. There was no effect of gender on any of these variables (all ps > 0.195).



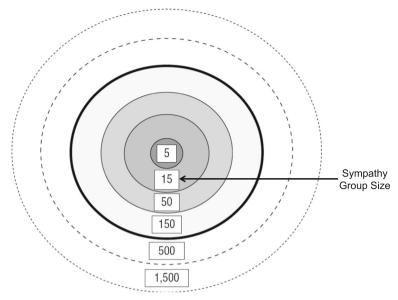


Fig. 1 Social network schematic. Human social networks are conceptualized as inclusive and hierarchical "circles," or layers, that scale with emotional closeness and interaction frequency. The Sympathy Group, the second-most inner layer of a social network, comprises individuals with whom we can rely on for instrumental support and with whom one interacts frequently. The number within each circle reflects the average number of people typically comprised in the layer. Image adapted from Dunbar (2014)

As mentioned, SWM is distinct from non-SWM (as in prior work; Meyer et al. 2012), they were uncorrelated in this study, r(123) = 0.05, p > 0.250); that having been said, SWM involves general non-SWM processes. To probe the specificity of the SWM-Sympathy Group size association, we ran a linear regression analysis investigating the association between SWM and Sympathy Group size controlling for the general non-SWM elements of SWM (alphabetizing trials). Critically, the effect of SWM on Sympathy Group size held when controlling for non-SWM, but fell just short of conventional levels of statistical significance (SWM: $\beta = 0.17$, t = 1.94, p = 0.055; non-SWM: $\beta = 0.16$, t = 1.87, t = 0.065).

Finally, although not the focus of the current investigation, we explored the association between performance on the control (alphabetizing) trials and each SNSQ component for the interested reader. Results showed a trend association between performance on these control/non-SWM trials and Sympathy Group size (r(123) = 0.17, p = 0.054) and an unexpected significant positive association with Active Network size (r(123) = 0.21, p = 0.021). Given that SWM and non-SWM performance were uncorrelated, these results suggest that these two competencies may contribute to different aspects of Sympathy Group size.

Study 2

In sum, as hypothesized, we found that SWM significantly predicts Sympathy Group size in humans and, thus, may be a key social cognitive competence underlying the Social



Brain Hypothesis. Intrigued by these behavioural findings, we sought to conceptually replicate and extend this effect by looking at whether neural activity engaged during SWM trials (vs. control non-SWM trials) also predicts Sympathy Group size. Critically, this would elucidate the neural circuitry linking SWM capacity to Sympathy Group size and, thus, point to a possible neural network underlying the Social Brain Hypothesis.

Regarding our predictions, as noted, in the introduction, conventional working memory tasks consistently activate a lateral frontoparietal network, particularly the dorsolateral prefrontal cortex (DLPFC). SWM also activates this lateral frontoparietal network, as well as a medial frontoparietal network associated with mentalizing. Although the lateral and medial networks typically show anti-correlated brain activation, SWM engages both networks. However, of these regions, only neural activity in the dorsal medial prefrontal cortex (DMPFC) and medial prefrontal cortex (MPFC) in response to SWM correlates with social skills, such as perspective-taking, thus making them good candidate regions that may link SWM processes to Sympathy Group size (Meyer et al. 2012). For this reason, we predicted that neural activity in DMPFC and MPFC would be associated with Sympathy Group size.

Methods

Participants

We performed a secondary data analysis of a sample of 25 participants (15 females, mean age = 21.56 ± 2.5) who were paid \$100 for participation. (Note: the previous publication by Meyer et al. (2015) focused on neural correlates of SWM per se, whereas we are examining the association between SWM neural activity and social network size.) This sample size was determined because it provides adequate power to detect neural activation in response to our SWM task (Mumford and Nichols 2008), while still being feasible given fMRI data acquisition costs. All participants provided written informed consent and the study was conducted in accordance with local Institutional Review Board guidelines.

Procedure and Measures

As in Study 1, participants completed an on-line questionnaire to generate stimuli for the SWM task and, separately, reported on their Sympathy Group size. Approximately 2 weeks later, they were invited to the lab; participants first underwent a structural MRI scan (MP-RAGE) followed by three functional MRI scans during which they completed the SWM task (totalling 54 unique SWM trials and 54 non-SWM control trials). All trials were jittered in timing (within and between trial elements) and ordered according to Optimize Design (Wager and Nichols 2003).

Sympathy Group Size Measure (Lewis et al. 2011; Stiller and Dunbar 2007) This is a widely used measure to assess Sympathy Group size. Participants were asked to list all of the people with whom they had personal contact or communication within the past 7 days, excluding i) work colleagues seen only in a work environment (unless they considered them genuine friends), ii) contacts with professionals (such as doctors, plumbers, etc.), and iii) other casual acquaintances (e.g., brief encounters in a shop).



This method explicitly targets close friends and social partners, and excludes more casual social relationships.

fMRI Image Acquisition and Analysis Functional images were acquired on a 3 Tesla (T) Siemans Trio with a T2*-weighted echo-planar plus sequence covering 36 axial slices (TR/TE = 2000/25 ms, flip angle = 90 degrees, 64×64 matrix, 3 mm thick, FOV = 200). To aid in fMRI data registration, we also acquired a Magnetization Prepared Rapid Gradient Echo scan (MP- RAGE; TR/TE = 2170/4.33 ms, flip angle = 7 degrees, 256×256 matrix, 1 mm thick, 192 sagittal slices, FOV = 256).

Imaging data were analyzed in SPM8 (Wellcome Department of Cognitive Neurology, Institute for Neurology, London, UK). The following preprocessing steps were performed to prepare the fMRI data for statistical analysis. First, each EPI volume was realigned to the first EPI volume of each run. Second, the T1 structural volume was co-registered to the mean EPI. Third, to normalize the T1 structural volume to a common group-specific space (with subsequent affine registration to MNI space), we used the group-wise DARTEL registration method included in SPM8 (Ashburner 2007). Fourth, we normalized the EPI volumes to MNI space using the deformation flow fields generated in the previous step, which simultaneously re-sampled volumes (3 mm isotropic) and applied spatial smoothing (Gaussian kernel of 8 mm, full width at half maximum).

Next, each participant's preprocessed data was modeled as an event-related design in the general linear model framework. We modeled regressors for the delay period of the task, separately for SWM and non-SWM trials. Only trials correctly answered by participants were included in the regressor of interest. Regressors of no interest capturing 1) the portions of the task not related to the delay period, 2) delay periods for inaccurately answered trials and 3) 6 motion regressors for each of the motion parameters from image realignment, were included in the model. To isolate neural activity specific to SWM, we compared SWM to non-SWM delay period activation. Thus, neural predictors reflect activity specifically associated with SWM processes, rather than general working memory processes.

To create SWM neural predictor variables, we created spherical (10 mm radius) regions-of-interest (ROIs) centered around cluster peaks associated with SWM (Meyer et al. 2015; dorsomedial prefrontal cortex [DMPFC]: -6 57 39, medial prefrontal cortex [MPFC]: 6 63 9; left dorsolateral prefrontal cortex [IDLPFC]: -45 27 39, and right dorsolateral prefrontal cortex [rDLPFC] 45 27 39). Each DMPFC, MPFC, and DLPFC predictor variable is the mean parameter estimate, averaged across the voxels within the ROI, from the SWM vs. non-SWM contrast.

To examine whether brain areas associated with SWM predict Sympathy Group size, we conducted linear regression analyses with these contrasts entered as predictors of Sympathy Group size. We used Bonferroni adjusted alphas of 0.0125 for each test (0.05/4) to correct for multiple comparisons.

Results

Consistent with past research, participants had an average Sympathy Group size of 15 people (SD = 7). Linear regression analyses comparing neural activity during the SWM vs. control non-SWM trials showed that neural responses in the DMPFC, MPFC and



bilateral DLPFC significantly predicted Sympathy Group size. Importantly, only DMPFC and MPFC neural activation remained significant predictors of this network after applying Bonferroni adjusted alphas (Table 1). That is, those individuals who showed greater activation in brain areas uniquely supporting SWM reported more friends with whom they interacted in the past 7 days, thus confirming and extending the findings from Study 1 (Fig. 2).

Data Availability Data from Studies 1 and 2 will be made available to readers upon request.

Discussion

Humans and other primates are distinguished by the complex and dynamic social groups that they inhabit, as well as a relatively large brain-to-body size ratio. According to the Social Brain Hypothesis, these two observations are not unrelated. Rather, it is precisely the cognitive demands of social living that underlies the enlargement of the neocortex in humans and other primates. Although research indicates that brain size is associated with social network size, less is known about the precise social cognitive mechanisms that drive the brain size-social network size association.

Here we address this gap: Across two studies, we show that SWM—i.e., the ability to actively maintain and manipulate social information—constrains the size of one's close social network. In Study 1, we provide behavioural evidence showing that SWM performance is associated with the number of core friends (i.e., those who can be relied upon to provide higher-cost support and with whom one maintains fairly regular contact). In Study 2, we found that neural activation in DMPFC and MPFC, while engaging SWM, is associated with individual variation in Sympathy Group size. This observation is consistent with structural MRI research showing that individuals who remembered more characters' mental states from a story had a larger Sympathy Group and had greater cortical volume in mentalizing brain regions, including the MPFC (Lewis et al. 2011). Importantly, whereas prior work has focused primarily on correlating brain structure size with social network size (e.g., Powell et al. 2010), to our knowledge, this is the first functional imaging evidence supporting the Social Brain Hypothesis. This finding is important as it points to neural correlates of a specific social

Table 1 Linear regression results with medial prefrontal cortex (MPFC) and dorsomedial prefrontal cortex (DMPFC) neural responses to social working memory (vs. non-social working memory) predicting Sympathy Group size

	В	SE	β	t	p	95% CI for B	
MPFC	3.82	1.22	0.55	3.14	0.003	1.31, 6.34	
DMPFC	3.013	1.06	0.51	2.85	0.005	.83, 5.20	
rDLPFC	3.1	1.24	0.46	2.51	0.02	.54, 5.67	
1DLPFC	2.97	1.29	0.43	2.31	0.03	.31, 5.63	



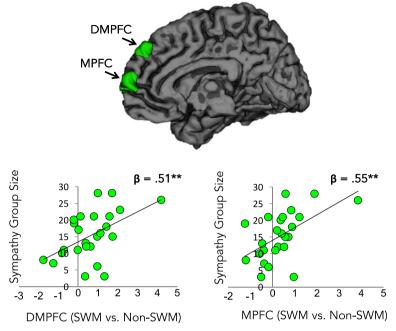


Fig. 2 Neural activation in DMPFC and MPFC in response to SWM (vs. non-SWM) predicts Sympathy Group size

cognitive ability that may underlie the brain size-network size association, a key tenant of the Social Brain Hypothesis.

In addition to showing that SWM constrains Sympathy Group size, we also gained some insight into the specificity of the SWM-Sympathy Group size relationship. As noted, human social networks are conceptualized as hierarchically inclusive "circles" that capture different relationship kinds varying in emotional closeness and frequency of contact (Zhou et al. 2005; Dunbar 2014). In Study 1, we found no association between SWM and the size of people's Active Network size—i.e., their more extended network (e.g., number of Facebook friends). We think this likely reflects the unique computational processes required in maintaining Sympathy Group relationships. People typically spend more time—and processing capacity—navigating interactions with close friends (vs. e.g., Facebook friends) and, consequently, computational errors for such relationships should entail greater social costs for the individual and the relationship. A close friend would likely be less tolerant than an Active Network friend if one organized a dinner at a steak house forgetting that the friend had become a vegetarian. Close friends should know and remember such things; that a friend would forget could be interpreted to reflect on the importance of the relationship. More generally, people want to be known, and prefer to interact with others who see them as they see themselves (e.g., Swann et al. 1994; Swann et al. 2003).

One question raised by these findings concerns the relative contributions of SWM and more general non-social working memory processes in supporting social network size. As noted, SWM assesses the ability to maintain and manipulate varying amounts of social information. Importantly, theory and prior research indicate that SWM is



supported by cognitive processes involved in non-SWM, as well as processes involved in mentalizing—it is thus distinct from, but overlaps with, general non-SWM. Of note, the association between SWM and Sympathy Group size in Study 1 held when controlling for non-SWM task performance, which suggests that aspects of SWM beyond what SWM shares with other measures of cognitive performance specifically relate to the size of one's Sympathy Group. Moreover, in Study 2, we found that neural responses to SWM task performance in brain regions associated with non-SWM (DLPFC) as well as SWM (DMPFC and MPFC) were associated with Sympathy Group size. Critically, however, only the brain regions preferentially associated with SWM (DMPFC and MPFC) remained significant predictors of Sympathy Group when adjusting alphas for multiple comparisons. Taken together, these data suggest that SWM is an important mechanism underlying the Social Brain Hypothesis. However, SWM is likely not the *only* mechanism that relates to social network size. Indeed, as Stiller and Dunbar (2007) observed, memory capacity for factual information also appears to limit the size of one's core friend group. Consistent with this, in Study 1, we found that performance on the control non-SWM trials was associated with Active Network size. Future work is needed to elucidate the complex interplay between cognitive skills that contribute to the various components of the social network.

Another point worth noting is that we indexed SWM using a task that assesses people's ability to maintain and manipulate information about friends' traits (in fact, this is the only SWM task available to date). However, reasoning about friends' traits is not the only form that SWM can take. For example, keeping track of friends' perspectives during a conversation or the political beliefs of people we just met at a party represent other SWM process (Meyer and Lieberman 2012). Thus, future work could develop measures to assess different forms of SWM to examine the reliability of our findings. In addition, our SWM task does not differentiate between the maintenance and manipulation phases of SWM. Thus, future SWM paradigms could also tease apart maintenance versus manipulation of social information in working memory to investigate which aspects of SWM relate to different components of the social network.

Finally, there are some limitations of the present work that should be probed in future research. First, the sample size in the imaging study (Study 2) is somewhat small by current standards. Although ROI analyses like the ones used here are less susceptible to false positives as compared to 'whole-brain' fMRI analyses characterized by multiple comparisons, the findings from Study 2 should be replicated in a larger sample to ascertain the strength of the effect. In addition, our sample in Study 1 consisted of young adults, most of who were university students and, specifically, female undergraduate psychology students. In this initial investigation, we prioritized sample homogeneity to augment our statistical power to detect an effect (e.g., Funder et al. 2014), but future work is needed to investigate the association between SWM and Sympathy Group size in more diverse samples—specifically, samples that vary in age, educational background, socio-economic status, relationship status, gender and/or racial-ethnic background—to assess the generalizability of the effect and boundary conditions. Finally, we used different measures to assess Sympathy Group size. In Study 1, Sympathy Group was assessed using items from the SNSQ that loaded onto a component characteristic of Sympathy Group friendships—that is, core friends who provide "higher-cost" support and with whom one maintains regular contact. In Study 2, the Sympathy Group was measured explicitly by asking participants to list all the people,



excluding casual relationships, that one had personal contact with over the last week. Importantly, though, both measures fit the conceptual definition of Sympathy Group relationships, and both measures produced mean Sympathy Group sizes consistent with the theorized average of 15 people (Dunbar and Spoors 1995). Indeed, the use of different Sympathy Group size measures can be seen as a strength since it demonstrates the generalizability of the SWM-Sympathy Group size association.

In conclusion, we have identified a specific social-cognitive competency—SWM—that predicts the number of people with whom one can successfully maintain a relationship. Of note, we have conceptualized SWM as a predictor of social network size—people have more (or less) friends because that is what their brain can computationally handle. Of course, it is likely that the number of friends we have—likely a function of many factors—contributes to SWM capacity, a question to be investigated in future work. Future work may also test whether, in addition to predicting the size of peoples' social network, SWM mechanisms relate to the role(s) people play in their network. For example, some individuals tend to be *nodes* connecting multiple friend circles (Barnes 1954). Perhaps those individuals with superior SWM not only have larger social networks but also are more likely to play a central, connecting role in those networks. We hope this work inspires future research on SWM and social network size and the (social) cognitive underpinning of the Social Brain Hypothesis more generally.

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Author Contributions The study concept and designs were developed by S. A. Krol and J. A. Bartz (Study 1) and by M. L. Meyer and M. D. Lieberman (Study 2). Testing and data collection was performed by S. A. Krol (Study 1) and M. L. Meyer (Study 2). S. A. Krol and J. A. Bartz performed the data analyses and interpretation for Study 1. M. L. Meyer performed the data analyses for Study 2 and M. L. Meyer and M. D. Lieberman performed interpretation for Study 2. S. A. Krol and M. L. Meyer drafted the manuscript, and J. A. Bartz and M. D. Lieberman provided critical revisions. All authors approved the final version of the paper for submission.

Compliance with Ethical Standards

Declaration of Conflicting Interests The authors declare no conflicting interests.

References

Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *NeuroImage*, 38(1), 95–113. https://doi.org/10.1016/j.neuroimage.2007.07.007.

Barnes, J. A. (1954). Class and committees in a Norwegian Island parish. *Human Relations*, 7(1), 39–58. https://doi.org/10.1177/001872675400700102.

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, 22(6), 469–493. https://doi.org/10.1016/0047-2484(92)90081-J.



- Dunbar, R. I. (1993). Coevolution of neocortical size, group size and language in humans. Behavioral and Brain Sciences, 16(04), 681–694.
- Dunbar, R. I. (1998). The social brain hypothesis. Brain, 9(10), 178–190.
- Dunbar, R. I. M. (2014). The social brain: psychological underpinnings and implications for the structure of organizations. Current Directions in Psychological Science, 23(2), 109–114. https://doi.org/10.1177 /0963721413517118.
- Dunbar, R. I. M., & Spoors, M. (1995). Social networks, support cliques, and kinship. Human Nature, 6(3), 273–290. https://doi.org/10.1007/BF02734142.
- Funder, D. C., Levine, J. M., Mackie, D. M., Morf, C. C., Sansone, C., Vazire, S., & West, S. G. (2014). Improving the dependability of research in personality and social psychology: recommendations for research and educational practice. *Personality and Social Psychology Review*, 18(1), 3–12. https://doi.org/10.1177/1088868313507536.
- Gusnard, D. A., Raichle, M. E., & Raichle, M. E. (2001). Searching for a baseline: functional imaging and the resting human brain. *Nature Reviews. Neuroscience*, 2(10), 685–694. https://doi.org/10.1038/35094500.
- Hill, R. A., & Dunbar, R. I. (2003). Social network size in humans. Human Nature, 14(1), 53-72.
- Kanai, R., Bahrami, B., Roylance, R., & Rees, G. (2012). Online social network size is reflected in human brain structure. *Proceedings of the Royal Society B: Biological Sciences*, 279(1732), 1327–1334. https://doi.org/10.1098/rspb.2011.1959.
- Lewis, P. A., Rezaie, R., Brown, R., Roberts, N., & Dunbar, R. I. M. (2011). Ventromedial prefrontal volume predicts understanding of others and social network size. *NeuroImage*, 57(4), 1624–1629. https://doi. org/10.1016/j.neuroimage.2011.05.030.
- Meyer, M. L., & Lieberman, M. D. (2012). Social working memory: neurocognitive networks and directions for future research. *Frontiers in Psychology*, *3*, 571. https://doi.org/10.3389/fpsyg.2012.00571.
- Meyer, M. L., Spunt, R. P., Berkman, E. T., Taylor, S. E., & Lieberman, M. D. (2012). Evidence for social working memory from a parametric functional MRI study. *Proceedings of the National Academy of Sciences*, 109(6), 1883–1888. https://doi.org/10.1073/pnas.1121077109.
- Meyer, M. L., Taylor, S. E., & Lieberman, M. D. (2015). Social working memory and its distinctive link to social cognitive ability: an fMRI study. Social Cognitive and Affective Neuroscience, 10, 1338–1347. https://doi.org/10.1093/scan/nsv065.
- Miyake, A., & Shah, P. (Eds.). (1999). Models of working memory: mechanisms of active maintenance and executive control. Cambridge: Cambridge University Press.
- Mumford, J. A., & Nichols, T. (2008). Power calculation for group fMRI studies accounting for arbitrary design and temporal autocorrelation. *NeuroImage*, 39(1), 261–268. https://doi.org/10.1016/j. neuroimage.2007.07.061.
- Powell, J. L., Lewis, P. A., Dunbar, R. I. M., García-Fiñana, M., & Roberts, N. (2010). Orbital prefrontal cortex volume correlates with social cognitive competence. *Neuropsychologia*, 48(12), 3554–3562. https://doi.org/10.1016/j.neuropsychologia.2010.08.004.
- Stiller, J., & Dunbar, R. I. M. (2007). Perspective-taking and memory capacity predict social network size. Social Networks, 29(1), 93–104. https://doi.org/10.1016/j.socnet.2006.04.001.
- Swann Jr, W. B., De La Ronde, C., & Hixon, J. G. (1994). Authenticity and positivity strivings in marriage and courtship. *Journal of personality and social psychology*, 66(5), 857.
- Swann Jr, W. B., Rentfrow, P. J., & Gosling, S. D. (2003). The precarious couple effect: Verbally inhibited men+ critical, disinhibited women= bad chemistry. *Journal of Personality and Social Psychology*, 85(6), 1095.
- Tabachnick, B. G., & Fidell, L. S. (2007). Using multivariate statistics (5th ed.). Boston: Pearson Education Inc. Retrieved from https://scholar.google.com/scholar_lookup?title=Using%20multivariate%20 statistics&author=Tabachnick&publication_year=2007.
- Wager, T. D., & Nichols, T. E. (2003). Optimization of experimental design in fMRI: a general framework using a genetic algorithm. *Neuroimage*, 18(2), 293-309.
- Zhou, W.-X., Sornette, D., Hill, R. A., & Dunbar, R. I. M. (2005). Discrete hierarchical organization of social group sizes. *Proceedings of the Royal Society B: Biological Sciences*, 272(1561), 439–444. https://doi. org/10.1098/rspb.2004.2970.

