Dorsomedial prefrontal cortex (DMPFC) prioritizes social learning during rest

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Abstract

Sociality is a defining feature of the human experience: we rely on others to ensure survival and cooperate in complex social networks to thrive. Are there brain mechanisms that help ensure we quickly learn about our social world to optimally navigate it? We tested whether portions of the brain's default network engage "by default" to quickly prioritize social learning during the memory consolidation process. To test this possibility, participants underwent functional magnetic resonance imaging (fMRI) while viewing scenes from the documentary film, *Samsara*. This film shows footage of real people and places from around the world. We normed the footage to select scenes that differed along the dimension of sociality, while matched on valence, arousal, interestingness, and familiarity. During fMRI, participants watched the "social" and "non-social" scenes, completed a rest scan, and a surprise recognition memory test. Participants showed superior social (vs. non-social) memory performance and the social memory advantage was associated with neural pattern reinstatement during rest in the dorsomedial prefrontal cortex (DMPFC), a key node of the default network. Moreover, it was during *early* rest that DMPFC social pattern reinstatement was greatest and predicted subsequent social memory performance most strongly, consistent with the "prioritization" account. Results simultaneously update 1) theories of memory consolidation, which have not addressed how social information may be prioritized in the learning process and 2) understanding of default network function, which remains to be fully characterized. More broadly, the results underscore the inherent human drive to understand our vastly social world.

Significance Statement

Writer Kurt Vonnegut once said "if you describe a landscape or a seascape, or a cityscape, always be sure to include a human figure somewhere in the scene. Why? Because readers are human beings, mostly interested in other human beings." Consistent with Vonnegut's intuition, we found that the human brain prioritizes learning scenes including people, more so than scenes without people. Specifically, as soon as participants rested after viewing scenes with and without people, the dorsomedial prefrontal cortex of the brain's default network immediately repeated the scenes with people during rest to promote social memory. The results add new insight into the human bias to process the social landscape.

As we move through everyday life, we come across an abundance of information. Just as an example, imagine walking through your favorite city. At once, you are bombarded with signs, shops, and people interacting in all kinds of ways. We continuously perceive far more than we could possibly remember (1-3), which is why some experiences stick with us and others are forgotten (4). Is certain information from our seemingly seamless encoding prioritized in memory, and if so, how?

One possibility is that social information—that is, information about people—may be prioritized in memory. Given that primates rely on conspecifics to ensure survival (5-8), social information is highly valuable (9), which should amplify its memorability (10-12). There is also evidence that social content tends to be easily learned and retrieved (13-14). For instance, the same stimuli is more memorable if participants attend to its social (vs. non-social) aspects during encoding (13, 15). Past social stressors (e.g., a romantic break-up) are also more easily re-experienced than past non-social stressors (e.g., a physical injury), even when the events are matched on emotional intensity at the time of the event (16). Social information can even be used to potentiate reinforcement learning as early in development as infancy (14). Collectively, psychological data point to the possibility that social information carries a powerful memorial glue.

If social information is privileged in memory, how might the brain prioritize it during the learning process? An answer to this question may stem from two observations. First, the brain region most reliably associated with social information processing, the dorsomedial prefrontal cortex (DMPFC; (17-20)), is also part of the brain's default network, known to engage quickly by default during rest (21-23). Second, rest is a time when new information is committed to memory (i.e., consolidated; (24-26)). The tendency for the human brain to "default" back to the DMPFC as soon as our mind is free of external demands may therefore bias us towards social learning during rest.

Consistent with this possibility, past work implicates DMPFC in social memory encoding and retrieval (15, 17, 27) and DMPFC may play a general role in social learning during rest (28-29). For example, DMPFC increases functional connectivity with other portions of the default network after encoding new social information, and this increased connectivity predicts social (but not non-social) subsequent memory performance (28-29). Critically, however, past work examining social consolidation at rest fully separates social encoding from non-social encoding to isolate which brain regions consolidate the different information at rest. As a result, it is impossible to know if social consolidation is "prioritized" at rest by the DMPFC based on prior research; a claim for prioritization would require evidence that when presented with social and non-social information during the same encoding session, the DMPFC prefers to consolidate the social information during subsequent rest, and possibly does so more quickly than brain regions consolidating other forms of information. Establishing the prioritization of social consolidation would update existing theories of learning and memory, which to date have not considered this possibility. This gap is surprising, given that theoretical accounts of memory formation suggest goal-relevant content may be prioritized during consolidation (30) and that humans have a strong, endogenous goal to feel connected to their social world (31).

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The hypothesis driving the present study is that social information is prioritized during consolidation at rest in the DMPFC. Strong evidence for this possibility requires anticipating and thwarting two potential confounds. First, social information is often conflated with a number of dimensions known to enhance memory: valence, arousal, interestingness and familiarity (32-34). If we found that the DMPFC consolidated social memory early in rest, it would be hard to know if it is the "socialness" of the information encoded (i.e., the extent to which it pertained to people) that drove prioritization versus the other dimensions with which socialness tends to covary. Second, to best approximate real-world social learning, it is important to use encoding stimuli that are as naturalistic as possible, yet a great deal of naturalistic social stimuli used in neuroscience research takes the form of a narrative story (35). Many naturalistic approaches to investigating the role of the default network in social cognition involve television dramas, movies, and podcasts (36-40). However, the narrative plot of these stories creates a confound for the present hypotheses. If participants encoded a story while undergoing fMRI and it was discovered that they had better memory for the social (vs. non-social) information in the story and that the DMPFC prioritized social consolidation at rest, it would be difficult to determine whether the social memory advantage was due to the prioritization of social learning at rest broadly speaking or whether the plot of the story creates a schema for social information (but not non-social information), which could incidentally improve and prioritize social memory.

To rule out these confounds, we presented participants with footage from the documentary film, *Samsara*. This documentary was intentionally developed to have no narrative or plot, and instead portrays footage of real people, places, and objects from around the world. Scenes from the documentary were normed by independent raters on valence, arousal, interestingness, familiarity, and socialness (i.e., the extent to which they had to do with people). This allowed us to select a subset of video clips that varied on the dimension of sociality, while being matched on the other dimensions. With this paradigm in hand, we had a new sample of participants complete functional magnetic resonance imaging (fMRI) while they encoded the social and non-social video clips in a fully intermixed fashion, completed a resting state scan, and a surprise memory test for the footage (Figure 1A).

If the social prioritization account is correct, we would expect to see the following patterns in our data. First, participants should show better memory performance for the social vs. non-social stimuli. Second, we should see evidence that the DMPFC preferentially consolidates the social information encoded (but not non-social information encoded), and this consolidation may occur during early stages of rest. This would be consistent with the idea that our tendency to default back to DMPFC as soon as we rest biases the brain towards social learning. We used the recently developed neural pattern reinstatement approach to test this hypothesis (41-42). This approach tests whether reengaging multivariate patterns from encoding during subsequent rest predicts memory performance (41). The reinstatement approach is conceptually similar to the idea of "replay" during rest from the rodent literature on memory consolidation (43-46).

To complement our hypotheses about the DMPFC in social consolidation, we also investigated whether pattern reinstatement in a prefrontal brain region traditionally associated with non-social memory—the left ventrolateral prefrontal cortex (lVLPFC; 47) —may show evidence of neural

pattern reinstatement during rest for the non-social (but not social) stimuli. Given that lVLPFC is not a region that shows quick activity by default during rest, we predicted lVLPFC would show non-social reinstatement across the rest period generally, as opposed to prioritization during early rest in particular. Finally, given that the hippocampus is thought to play a general role in memory consolidation (24, 48), we also examined whether this brain region shows evidence of both social and non-social memory consolidation during rest.

RESULTS

Better Memory Performance for Social (vs. Non-Social) Videos

Our first prediction is that participants will show better memory performance on the surprise memory test for the social (vs. non-social) video clips from *Samsara*. The surprise memory test was structured such that participants were shown images from the 60 encoded (30 social; 30 non-social) and 60 lure video clips (30 social; 30 non-social) in a fully randomized order. The lure video clips were normed on valence, arousal, interestingness, and familiarity in the same fashion as the encoded stimuli (see Methods). Consistent with our first prediction, participants showed superior social (vs. non-social) memory performance (paired sample $t(24)=5.055$, $p=3.612e-05$; Figure 1b). We defined memory performance here as the d' memory score (by subtracting standardized false alarms from standardized hits with z-scores derived via the inverse cumulative density function) divided by the correct reaction time (RT) so that our memory performance score considers both accuracy and speed. It is noteworthy that social memory performance remains significantly better than non-social memory performance even if we only consider d' as our measure of accuracy (paired sample $t(24)=5.090$, $p=3.735e-05$) or just correct RT as our measure of accuracy (paired sample $t(24)=-2.873$, $p=8.595e-03$). Thus, the behavioral results robustly suggest social information is better recalled than non-social information, even when constructs often conflated with sociality (i.e., valence, arousal, interestingness, and familiarity) are held constant.
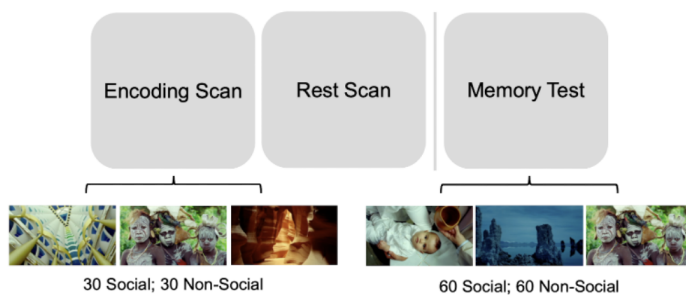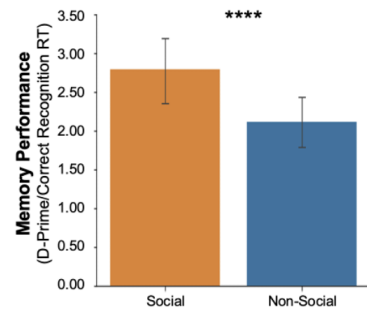

Figure 1. A) Experimental Paradigm. Participants encode social and non-social video clips from Samsara in a randomized order and a subsequent rest scan. Next, participants complete a surprise recognition memory test that includes all of the 60 videos encoded, as well as 60 lure videos that were not previously encoded. Social and non-social videos are matched on valence, arousal, interestingness, and familiarity and differ on the dimension of sociality: the extent to which

they have to do with people. B) Memory Performance. Participants demonstrated better social versus non-social memory performance.

Double-Dissociation for Social (DMPFC) and Non-Social (lVLPFC) Consolidation Mechanisms during Rest

We created regions-of-interest (ROIs) of the DMPFC cluster observed in the contrast of social (vs. non-social) encoding and the lVLPFC cluster observed in the contrast of non-social (vs. social) encoding (Figure 2A; see Methods for information on ROIs). Each subject's multivariate pattern in the ROIs during social video encoding, and separately, non-social video encoding were extracted. Next, we performed the reinstatement analysis developed by Schapiro & Norman (41; Figure 2B). The approach, conceptually, is template matching: identifying instances during rest in which the multivariate DMPFC pattern is meaningfully similar to the pattern observed during encoding and linking the number of reinstatements to subsequent memory performance (see Methods for more details). The observed reinstatement events showed high correlations with encoding patterns (Means > 0.585; SDs < 0.0644), which further supports and justifies counting these instances as reinstatement.
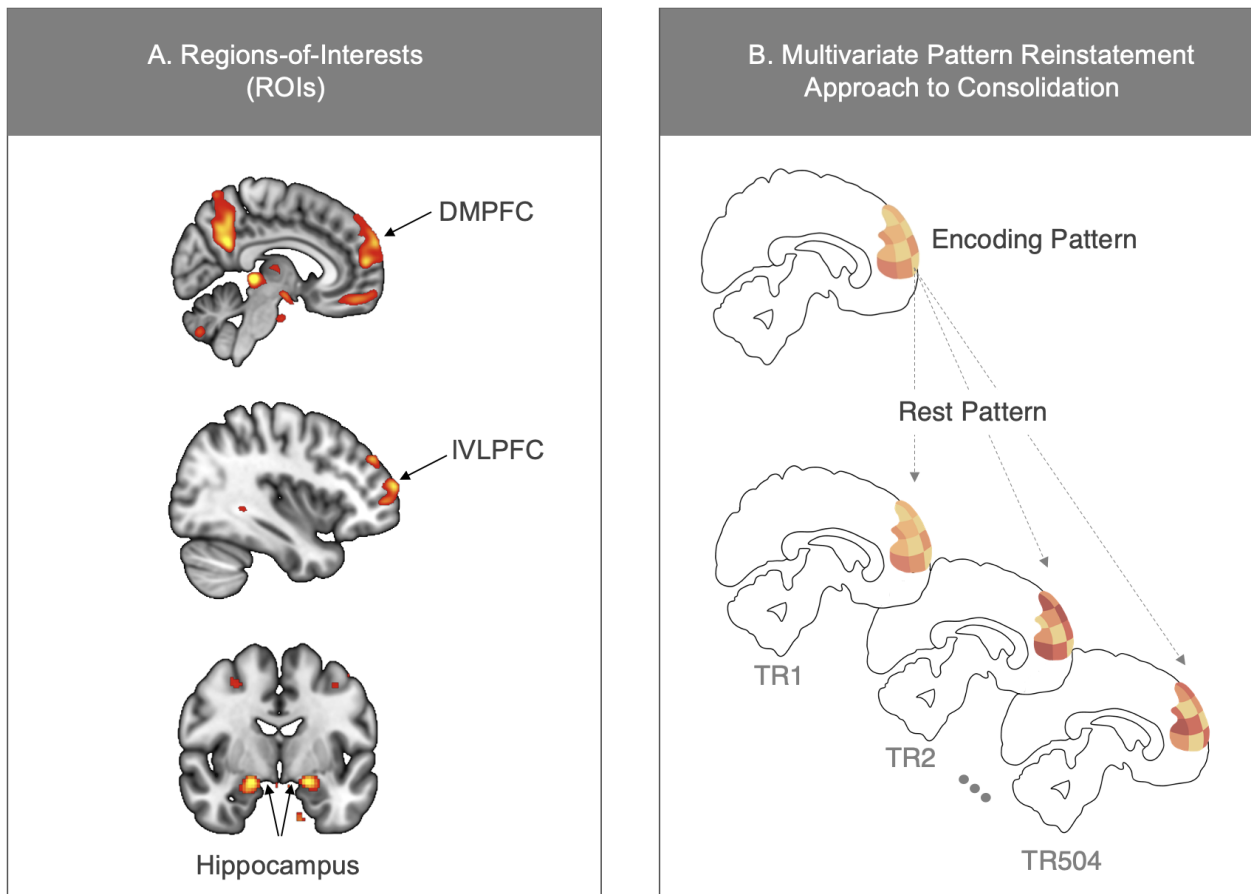

Figure 2. A) Regions-of-interest (ROIs) predicted to show reinstatement and subsequent memory effects. DMPFC refers to the dorsomedial prefrontal cortex, which was predicted to show social reinstatement and subsequent social memory effects. lVLPFC refers to the left ventrolateral prefrontal cortex and was predicted to show non-social reinstatement and subsequent non-social

memory effects. The hippocampus, given its broad role in memory, was predicted to show reinstatement and subsequent memory effects collapsed across social and non-social content. B) Visual depiction of the reinstatement approach in which the multivariate patterns in a ROI during encoding are applied to each TR of the subsequent rest scan. In line with prior work (41), correlations between the encoding pattern and TR rest pattern that are 1.5 standard deviations above the mean for a given subject are considered instances of reinstatement.

Consistent with the prediction that DMPFC preferentially consolidates social information, the number of DMPFC social pattern reinstatements across the rest period correlated with social memory performance (r=0.43, p=0.042; Figure 3A) whereas the number of non-social pattern reinstatements in DMPFC across the rest period was unrelated to non-social memory performance (r=-.14, p=0.505, Figure 3A). The lVLPFC showed the opposite pattern of results. The number of lVLPFC non-social pattern reinstatements significantly correlated with better non-social memory performance (r=0.44; p=0.029; Figure 3B) whereas the number of lVLPFC social pattern reinstatements was unrelated to social memory performance (r=-0.05; p=0.824; Figure 3B). It is noteworthy that, overall, there was a greater number of non-social (vs. social) DMPFC pattern reinstatements (paired samples t(23)=-2.450, p=0.023; mean social DMPFC=29.00 SD=10.85; mean non-social DMPFC=39.96 SD=12.01), although as noted above and shown in Figure 3A, the number of non-social DMPFC pattern reinstatements do not significantly relate to non-social memory performance (whereas the number of DMPFC social pattern reinstatements do significantly relate to social memory performance).

Although our hypotheses were specific to the DMPFC and VLPFC, to ensure we did not miss any meaningful patterns in other brain regions, we ran two follow-up analyses. First, we assessed whether the relationship between the number of neural pattern reinstatements during rest and subsequent memory was significant in the other ROIs observed during encoding (social vs. non-social encoding: VMPFC; precuneus, left amygdala and fusiform gyrus; non-social vs social encoding: bilateral parahippocampal place area). None of these follow-up analyses were significant (r's < 0.208, p's > 0.318), except for the lPPA showing a significant (and negative) non-social reinstatement-to-subsequent non-social memory relationship (r=-.539, p=0.007). Second, given that it is possible regions outside of those observed during encoding could show evidence of reinstatement-to-subsequent memory effects, we next repeated our reinstatement analyses with a k=50 whole-brain parcellation (49). No additional brain regions showed support for this possibility. Collectively, these results suggest that the link between greater neural pattern reinstatement during rest and superior subsequent memory is supported by different prefrontal regions for social (DMPFC) and non-social (lVLPFC) memory.

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A. DMPFC Reinstatement – Memory Relationships
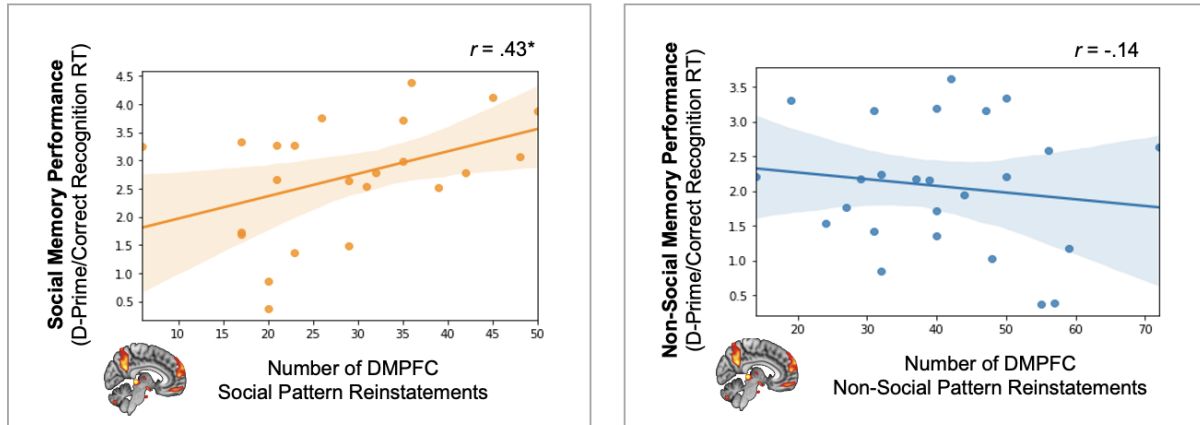
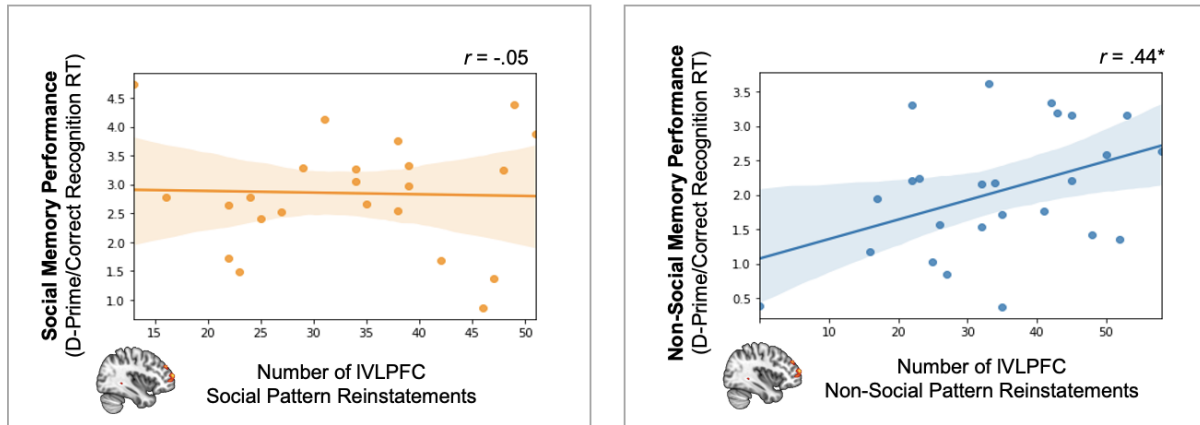
B. lVLPFC Reinstatement – Memory Relationships

Figure 3. Double-dissociation for social and non-social memory consolidation. Panel A) shows that DMPFC social pattern reinstatement significantly predicts social, but not non-social, memory performance. Panel B) shows that lVLPFC non-social pattern reinstatement significantly predicts non-social, but not social, memory performance.

The DMPFC Shows Evidence of Social Consolidation during Early Stages of Rest

Given that we established a double dissociation such that DMPFC social pattern reinstatements relate to social (but not non-social) memory performance, while lVLPFC non-social pattern reinstatements relate to non-social (but not social) memory performance, we next sought to dig deeper into how DMPFC may prioritize social learning during rest. The definition of "prioritize" is to treat something as more important than other things. Our next question was whether the brain prioritizes DMPFC social pattern reinstatement by doing it early in the consolidation process. That is, does social consolidation happen quickly in the DMPFC? To examine this possibility, we simply divided our resting state scan into early (0-168 seconds), middle (168-336 secs), and late (336-504 secs) time periods and summed the number of DMPFC social pattern reinstatements in each time period. We then used a linear mixed effects model to test the within-subjects contrast that the number of reinstatements during the early portion of rest is significantly greater than the middle and late rest periods (i.e., $2/3_{early}$ -$1/3_{middle}$ -$1/3_{late}$), which was significant ($t(44)=3.043$, $p=0.004$;

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Figure 4). Moreover, the relationship between the number of DMPFC social pattern reinstatements and social memory performance is driven by early rest: when DMPFC social pattern reinstatement for early, middle, and late rest were entered as separate regressors in a model predicting social memory performance, only early rest significantly predicted social memory performance ($F(2,44)$=9.771, p=0.006). Follow-up correlation analyses further confirmed this effect, showing the correlation is significant during the early rest period (r=0.580, p=0.004) but not the middle (condition-level r=0.115, p=0.600) or late rest periods (r=0.188, p=0.391, Figure 5).
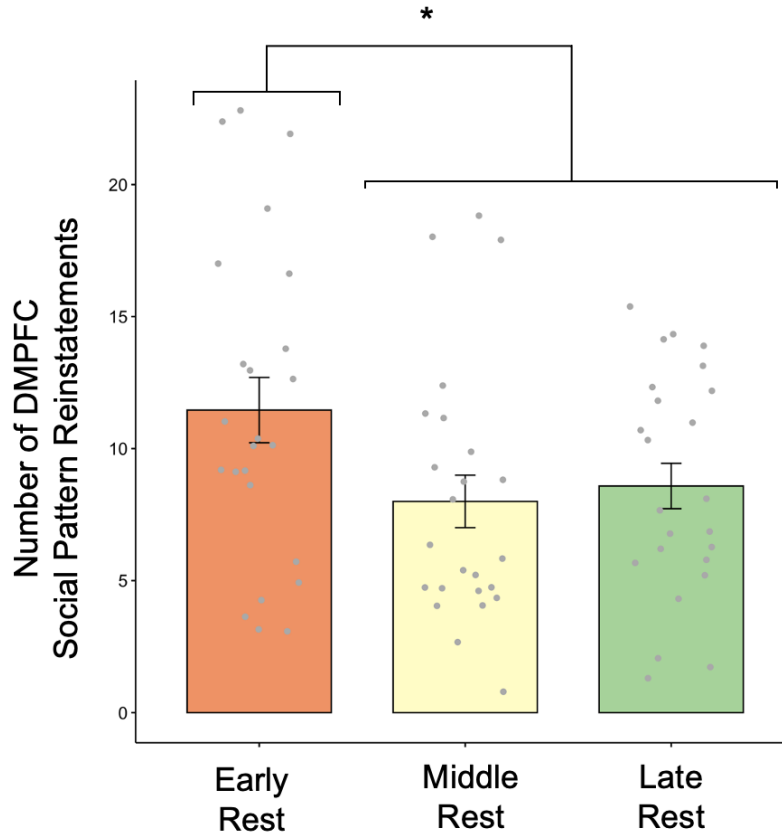

Figure 4. DMPFC shows a greater number of social pattern reinstatements during early (vs. middle and late) portions of the rest scan.

The same analysis with the non-social DMPFC encoding template produced null results: the number of non-social pattern reinstatements in DMPFC was not greater during early vs. middle and late periods of rest ($t(44)$=1.459, p=0.152). Additionally, the number of non-social pattern reinstatements in DMPFC was unrelated to non-social memory performance during early, middle, and late rest periods (r's<0.259, p's>0.211). Overall, the temporal analyses add further support for the prioritization hypothesis: it is earlier moments of rest in which social information is preferentially consolidated by the DMPFC at rest.

In contrast to the DMPFC, the lVLPFC did not show evidence of temporal prioritization for non-social consolidation. There was not a greater number of non-social lVLPFC pattern reinstatements during early (vs middle and late) rest periods ($t(46)$=0.895, p=0.376). Moreover, the correlation between lVLPFC non-social pattern reinstatement and non-social memory

performance was marginal during all time-periods (early r=0.300, p=0.145; middle r=0.375, p=.065; late r=0.312, p=0.130), indicating the non-social consolidation relationship was not unique to early rest. In other words, while lVLPFC non-social pattern reinstatement does preferentially relate to non-social memory consolidation, it does not show evidence of early prioritization.
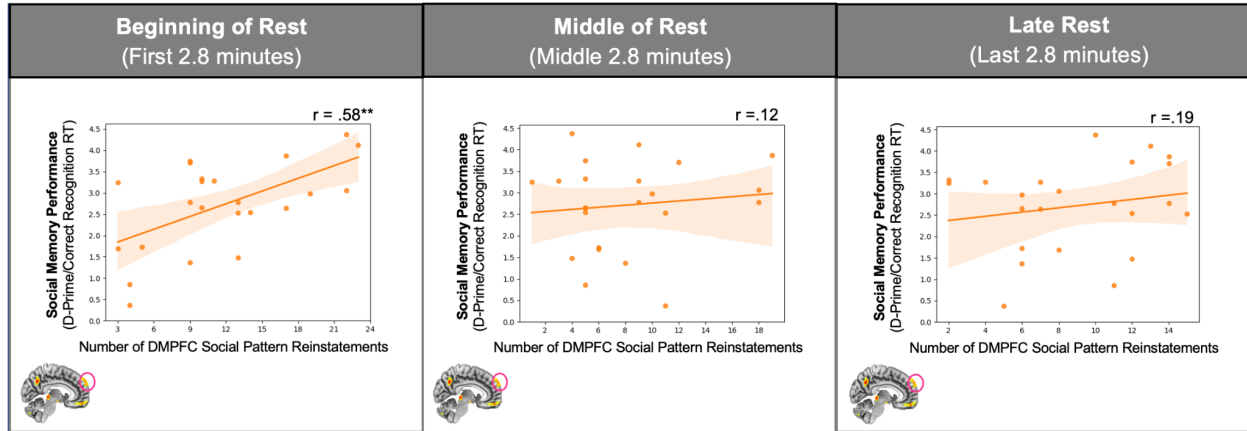

Figure 5. The relationship between DMPFC social pattern reinstatement and subsequent social memory is driven by the early rest period.

The Hippocampus Plays a General Role in Memory Consolidation at Rest

Given its broad role in memory consolidation (50), we next examined the hippocampus. Regions-of-interest were created from a correct vs. incorrect contrast at encoding where clusters emerged in both the left and right hippocampus. A multivariate pattern template for correctly remembered stimuli was extracted from encoding data within each ROI and used for pattern reinstatement analysis. Consistent with previous literature (41), we found a marginal effect indicating that the amount of correct pattern reinstatement in the right hippocampus at rest was negatively correlated with overall memory performance (r=-0.396, p=0.061). Looking at each type of memory separately, we found a non-significant relationship between social correct pattern reinstatement and social memory performance (r=0.228, p=0.295), as well as non-social correct pattern reinstatement and non-social memory performance (r=-0.365, p=0.087) in the right hippocampus. Additionally, the amount of correct pattern reinstatement was not greater in earlier (vs middle and late) rest periods (t(46)=0.553, p=0.582).

Mean Encoding Results

Past work has demonstrated "encoding and subsequent memory" effects such that greater activation during encoding often predicts superior subsequent memory (51-53). It is therefore possible that our reinstatement results are epiphenomenal, reflecting residual effects driven by encoding. Given this possibility, we sought to explore if mean activation at encoding of social and non-social stimuli meaningfully predict participants' memory scores and, if yes, to delineate the ways in which brain activity at encoding and brain activity during post-encoding rest uniquely contribute to participants' memory performance. We found, however, that neither mean activation in the DMPFC in response to social stimuli (r=0.113, p=0.607) nor in the lVLPFC in response to non-social stimuli (r=-0.321, p=0.109) significantly related to participants' subsequent memory performance. We hypothesize that this difference between our results and prior work could be

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driven by the greater complexity in the stimulus set than in previously used paradigms, and the lack of a narrative structure in the stimulus set in comparison to other naturalistic stimuli designs. Overall, these follow-up analyses further point to the important role of post-encoding rest in memory consolidation, with the temporal prioritization of social memory consolidation by the DMPFC.

DISCUSSION

Humans are a highly social species and must learn from their social environment to succeed in everyday life (43). Yet, whether and how the brain may be tuned towards social learning remains unclear. We provide the first evidence that the DMPFC prioritizes social learning via quick-acting consolidation processes during rest. In contrast, the lVLPFC, a region previously implicated in encoding and subsequent memory effects (47, 55-56), promotes non-social learning via consolidation mechanisms at rest in a non-prioritized fashion. Collectively, the findings suggest that social information may be preferentially prioritized during learning and update existing models of memory consolidation, which to date have not documented this possibility.

The findings provide key support for the suggestion that the human brain may be "social by default" (57-58). This perspective argues that, given that the same brain regions associated with social inference comprise a great deal of the default network, a brain system characterized by activating "by default" during rest, important social cognitive processes may occur by default during rest in humans to facilitate navigating social life (57-58). In particular, our results support this hypothesis by showing that the DMPFC, a key default network region, commits social memory traces immediately during rest. Thus, the tendency to engage DMPFC "by default" during rest may keep the brain in a prepared state to facilitate social learning.

Whether such default social tuning mechanisms help ensure we are socially savvy versus the possibility that social brain mechanisms engage by default as a consequence of people tending to be very social remains to be determined. On the one hand, default network engagement at rest has been observed early in infant development (59), suggesting humans may come into the world with default network mechanisms in place to help ensure sociality. On the other hand, transitioning into contexts that amplify the need for social bonding and new social roles, such as the transition into adolescence as well as the transition to motherhood, correspond with systematic changes in default network function, including resting state patterns (60-62). Whether such changes reflect purely environmental versus biological mechanisms remains to be fully determined. At the very least, future work could examine how manipulating social contact impacts default social learning patterns.

The DMPFC social consolidation results are consistent with recent arguments of adaptive memory consolidation (30), which suggest that post-encoding consolidation processes may prioritize goal-relevant information. This account has proposed multiple dimensions that may be prioritized during consolidation, such as valence and arousal (30). Note that our social and non-social stimuli were matched on valence and arousal, as well as other dimensions often conflated with sociality: interestingness and familiarity. Thus, sociality may be one dimension of many that

the brain 'tags' for adaptive memory processes. Relatedly, the default network includes multiple brain regions in addition to the DMPFC, including the VMPFC, precuneus, tempoparietal junction, and superior temporal sulcus extending into temporal poles. It is thus possible that while the DMPFC prioritizes social learning during rest, other default network regions may prioritize consolidating the types of content they respond to. Moreover, even within the DMPFC, some social dimensions may be more prioritized than others (e.g., cues of social connectedness versus cues of status). Future research can investigate the unique contributions of competing organizational dimensions for adaptive memory consolidation and how variability in social content may alter memory consolidation processes within the DMPFC.

Considerable work implicates the default network and, particularly, portions of the medial prefrontal cortex (MPFC) in schema instantiation (36, 63). Many of these findings have been observed while participants passively view audio or visual naturalistic narratives during encoding or reinstate similar neural patterns at recall. Relatedly, the DMPFC portion of MPFC preferentially responds to naturalistic narratives involving people (20) and participants with pre-existing, polarized social schemas show similar neural responding in DMPFC while viewing naturalistic, schema-relevant stimuli (38, 64). Our results suggest neural patterns for schema-specific events may be reinstated during consolidation in post-encoding rest to facilitate subsequent memory performance. Indeed, recent findings suggest that fictional narratives "linger" in mind post-encoding (65), further pointing to the possibility that stories about people may stick with us, in part, via post-encoding consolidation mechanisms.

Additionally, prior memory research suggests that default network activity during encoding relates to higher-order, more abstract schema representations that occur on the timescale of minutes (66). In the current study, we demonstrate that DMPFC activity during consolidation benefits subsequent memory performance within an experimental stimulus design that lacks any coherent narrative structure across time. It is possible, however, that participants in our study activated relevant schemas during encoding on a much shorter time scale (on the order of seconds) to situate the video clips in a larger, perhaps self-relevant, context. If so, past suggestions that the default network, or at least DMPFC, supports longer-time scale processing may need to be revised, as it is possible that the cognitive processing needed in prior work (e.g., relating social inferences to existing schemas) co-occurs with longer-time scales intrinsic to narratives. In other words, when the narrative structure of social stimuli is removed, the DMPFC still preferentially responds to and consolidates social information and it does so quickly. To further probe this possibility, future work can systematically investigate more complex social narratives that require schema activation on shorter timescales. Our social worlds are complex and nuanced; they can require the integration of multiple, independent, co-occurring narratives during a large dinner party or professional networking event. Future work may aim to reveal if regions of the MPFC encode and juggle multiple schematic representations on shorter timescales within contexts of greater social complexity to benefit memory.

Findings from the current study contribute to a greater understanding of default network function. One current account of default network function proposes that the default network may process higher-order, internally constructed representations (67-68). Alternatively, to integrate findings

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that implicate the default network in social cognition, others have more recently proposed the default network may integrate extrinsic social information and intrinsic idiosyncratic information to facilitate a shared neural code across individuals (69). Results from our study propose one possible mechanism by which the default network may integrate extrinsic social information and intrinsic idiosyncratic information: via social cognitive consolidation functions at rest. Future work may seek to explore social and non-social higher-order reasoning tasks in order to parse competing accounts of default network function, as well as better elucidate mechanisms of social consolidation functions within the default network during rest.

We also observed pattern reinstatement in the hippocampus negatively correlated with overall memory performance (collapsing across social and non-social stimuli) in a non-prioritized fashion. This finding nicely dovetails the prior work our reinstatement approach was based on, which also found that hippocampal pattern reinstatement helps commit weakly learned information to memory (41). Specifically, Schapiro et al. (2018) required participants to learn three sets of novel shapes and found greater hippocampal reinstatement predicted better memory for the weakly learned shapes (i.e., a negative correlation between reinstatement and memory performance). Similarly, research in rodents examining hippocampal replay finds that the relationship between encoding and replay is not always positively correlated and that hippocampal replay may serve to build representations of the entire environment, rather than just the well-learned aspects (70).

Conclusion
In summary, we found that when left with the choice to consolidate social or non-social information, the human brain prioritizes consolidating the social information during rest. This process happens through the DMPFC, a key node of the brain's default network–which gets its name from the observation that it activates "by default" whenever our mind is free from external demands. Our results therefore suggest that the tendency to "default" to DMPFC may help ensure we learn new social information as soon as we can.

METHODS

Participants
Twenty-six individuals (17 females; mean age = 22.77, SD = 4.8) were recruited for participation in the study. All participants provided informed consent in accordance with the Dartmouth College Institutional Review Board. Participants were awarded course credit or paid $20 per hour for study completion.

Stimuli
Stimuli presented at encoding consisted of 5-10 second video clip excerpts from the non-narrative, documentary film, *Samsara*. A total of 60 video clips were presented at encoding, 30 of which were social stimuli (e.g., showed footage of humans) and 30 of which were non-social stimuli (e.g., showed footage of locations and industrial objects).

A total of 120 stimuli were selected based on ratings from mTurk participants (n=372) who previewed 389 video clips from *Samsara*. Participants were presented with 65 video clips and

rated each clip they saw on dimensions of familiarity, valence, pleasantness, excitement, and sociality. Ratings were made on a scale from 1-100 (where 1=low familiarity, low pleasantness, low excitement, or negative valence and 100=high familiarity, high pleasantness, high excitement, or positive valence). Mean ratings of familiarity, valence, pleasantness, and excitement were not statistically significantly different across social and non-social video clips (t's<0.59, p's>0.53), but mean ratings of sociality did significantly differ (Mean social videos = 71.60, SD = 9.43; Mean non-social videos = 34.63; SD = 6.58; t=-28.97; p=1.40e-36).

Procedures
Participants completed an fMRI scanning session consisting of a structural anatomical scan, two encoding scans, a post-encoding rest scan, and subsequently, a surprise memory test.

Encoding
To mimic the way we simultaneously encounter social and non-social information in everyday life, at encoding, social and non-social video clips were randomly presented, as opposed to being blocked. Jittered fixation occurred after each video clip (mean interstimulus interval (ISI) = 3.00 secs; SD = 0.825 secs). Each participant completed two (2) encoding functional runs lasting 11 minutes.

Resting State
Next, participants completed a resting state scan. At rest, participants were instructed to think about what they wanted and stay awake. Based on prior research examining consolidation during rest, each rest scan lasted 8.4 minutes (29, 71).

Memory Test
After the post-encoding resting state scan, participants completed a surprise memory test where they indicated if the image on the screen was shown to them at encoding by selecting 'Yes', 'No', or 'I don't know'. Participants had up to 6 seconds to respond, and were presented with 120 images of 60 social and 60 non-social stimuli. The test was made up of 60 true images shown at encoding, and 60 lure images taken from video clips of documentary film, *Samsara*, but not shown during the encoding phase. Stimulus images were randomly presented across participants. Our memory performance variable takes into account both accuracy and speed. Specifically, we calculated the d' memory score by subtracting standardized false alarms from standardized hits with z-scores derived via the inverse cumulative density function. This value was then divided by the speed (i.e., reaction time (RT)) with which it took participants to answer accurately (i.e., d'/correct RT).

fMRI Data Acquisition
Brain imaging was conducted at the Dartmouth Brain Imaging Center in Hanover, NH on a Siemens Prisma 3T scanner using a 32-channel head coil. Functional images were acquired with a T2*-weighted echo-planar imaging sequence set to the following parameters: voxel size = 2.5 x 2.5 x 2.5 mm, repetition time (TR) = 1000 ms, echo time (TE) = 30 ms, field of view (FoV) = 24 cm, slice thickness = 2.5-mm, matrix=96 x 96, flip angle=59°, multiband acceleration factor = 4. Each participant also underwent a T1-weighted structural image (voxel size=0.9-mm, TR = 2300

ms, TE = 2.32 ms, FoV = 24 cm, slice thickness=0.9-mm, matrix=256 x 256, and flip angle=8°). The study design consisted of an event-related randomized design determined by easy-optimize-x (72) to maximize detection of meaningful neural clusters from the linear contrasts of interest from encoding (i.e. social vs. non-social encoding), which later serve as regions-of-interest (ROIs) for reinstatement analyses.

fMRI Data Preprocessing
Results included in this manuscript come from preprocessing performed using fMRIPrep 20.2.2 (73-74; RRID:SCR_016216), which is based on Nipype 1.6.1 (75-76; RRID:SCR_002502). As recommended by the creators of fMRIprep, the preprocessing steps are reported below verbatim from the software output.

Anatomical Data Preprocessing
A total of 1 T1-weighted (T1w) images were found within the input BIDS dataset. The T1-weighted (T1w) image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (77), distributed with ANTs 2.3.3 (78, RRID:SCR_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 5.0.9, RRID:SCR_002823, 79). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (ANTs 2.3.3), using brain-extracted versions of both T1w reference and the T1w template. The following template was selected for spatial normalization: ICBM 152 Nonlinear Asymmetrical template version 2009c [80, RRID:SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym],

Functional Data Preprocessing
For each of the BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.9, 81). Susceptibility distortion correction (SDC) was omitted. The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying the transforms to correct for head-motion. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD reference was then co-registered to the T1w reference using flirt (FSL 5.0.9, 82) with the boundary-based registration (83) cost-function. Co-registration was configured with nine degrees of freedom to account for distortions remaining in the BOLD reference. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions, 84) and Jenkinson (relative root mean square displacement between affines, 81). FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by 84). The three global signals are extracted within the CSF, the WM,

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and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, 85). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. in that instead of eroding the masks by 2 pixels on BOLD space, the aCompCor masks are subtracted a mask of pixels that likely contain a volume fraction of GM. This mask is obtained by thresholding the corresponding partial volume map at 0.05, and it ensures components are not extracted from voxels containing a minimal fraction of GM. Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (86). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardised DVARS were annotated as motion outliers. The BOLD time-series were resampled into standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using antsApplyTransforms (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (87). Non-gridded (surface) resamplings were performed using mri_vol2surf (FreeSurfer).

General Linear Model
Neuroimaging data were analyzed using NLTools (88). The data were spatially smoothed using a 6mm full width half maximum 3D gaussian kernel. Nuisance variables included in the model consisted of 6 head motion parameters (x, y, and x directions of roll, pitch, and yaw rotations), a high-pass filter (duration 128 seconds), linear and quadratic filters, and run regressors. TRs in nonsteady-state and TRs with spikes in global signal and average frame difference greater than 3 SDs were included as individual regressors.

For functional data obtained during encoding scans, a general linear model was created for each participant to estimate task-induced activation during social and non-social stimulus presentation. Stimulus presentation regressors were convolved with a Glover hemodynamic response function. For functional data obtained during resting state scans, an additional intercept regressor was included to remove global signal (84). All resting state analyses were performed on the remaining residual time series.

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First-level contrasts comparing social and non-social stimuli at encoding were generated for each subject from the model-estimated data. Second-level analyses were subsequently performed to derive regions-of-interest (ROIs). These group contrasts were statistically thresholded at p < .001 with a cluster extent of 200 voxels. The social versus non-social contrast revealed significant clusters of activity in the DMPFC (x=12 y=52 z=40, k=501), VMPFC (x=4 y=52 z=-18, k=517), precuneus (x=6 y=-60 z=34, k=313), left amygdala (x=-20 y=-8 z=-14, k=16433), and left fusiform gyrus (x=-44 y=-50 z=-20, k=4572). The non-social versus social contrast revealed significant clusters of activity in bilateral parahippocampal place area (x=-34 y=-48 z=-2, k=1243; x=32 y =-40 z=-4, k=1149) and left VLPFC (x=-34 y=48 z=26, k=262).

An additional first-level contrast comparing activity during encoding of trials that were later correctly versus incorrectly remembered was generated for each subject. Second-level analyses were statistically thresholded at p < .001 with a cluster extent of 30 voxels, given the relatively small anatomical size of the hippocampus and to help ensure we had a hippocampal cluster to investigate. The correct versus incorrect contrast revealed significant clusters of activity in bilateral hippocampus (x=-20 y=-8 z =-16, k=36; x=20 y=-6 z=-18, k=38), and right parahippocampal Gyrus (x=32 y=-76 z=-22, k= 1504).

Follow-up whole brain analyses were performed using the k=50 whole brain parcellation that used k-means clustering to isolate meta-analytic coactivations from Neurosynth (89). This parcellation was chosen to help ensure that the regions selected are functionally relevant to psychological constructs. Whole brain reinstatement analyses were multiple comparisons corrected using a bonferroni-corrected p-value of 0.001.

Pattern Reinstatement
Multivariate template patterns were created using beta values extracted from functional ROIs identified in first-level contrasts at encoding. The multivariate template patterns from encoding were correlated with the multivariate template pattern within the same functional ROI for each TR during post-encoding rest (TRs=504), generating a matrix of correlation values for each template pattern across the duration of rest. Consistent with the research our approach is based on Schapiro et al. (41), a potential reinstatement was defined as a correlation greater than 1.5 SD above the mean of all correlations for a given subject. The amount of correlation values that exceeded this threshold were summed across post-encoding rest to generate a count metric used in subsequent analyses. Memory performance scores and reinstatement values from the full rest periods were excluded if greater than 2 SDs away from the group mean. Brain-behavior correlations reflect two-tailed p-values.

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