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Social Working Memory: Neurocognitive networks and plasticity

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Author
Meyer, Meghan Leigh

Publication Date
2014

Peer reviewed|Thesis/dissertation
Social Working Memory: Neurocognitive networks and plasticity

A dissertation submitted in satisfaction of the requirements for the degree Doctor of Philosophy in Psychology

by

Meghan Leigh Meyer

2014
The social world is incredibly complex and the ability to keep track of various pieces of social information at once is imperative for success as a social species. Yet, how humans manage social information in mind has to date remained a mystery. On the one hand, psychological models of working memory, or the ability to maintain and manipulate information in mind, suggest that managing social information in mind would rely on generic working memory processes. However, recent research in social neuroscience questions this possibility, as the same neural system, the medial frontoparietal system, that supports basic social cognitive processing disengages during working memory (McKiernan et al., 2003). In fact, a failure to decrease the medial frontoparietal system during working memory actually interferes with working memory performance (Anticevic et al., 2010). However, prior to this dissertation, no research had examined the neural mechanisms supporting the ability to maintain and manipulate social
cognitive information in mind, or engage in ‘social working memory’ (SWM). Thus, the goal of the present dissertation was to examine, for the first time, the extent to which SWM and non-social, cognitive working memory (CWM) rely on the same or different underlying neural mechanisms.

Paper 1 employed a novel SWM paradigm to examine which neural regions support SWM. In a within-subject design, participants (N=16) completed SWM trials that required them to consider two, three, or four of their friends along a trait dimension during a delay period while undergoing functional magnetic resonance imaging (fMRI). Linear increases in neural activity as a function of the number of friends considered (a response pattern characteristic of working memory systems (Rypma et al., 1999)) were found in two neurocognitive networks: the lateral frontoparietal system associated with CWM and the medial frontoparietal system previously associated with basic forms of social cognitive processing (Meyer et al., Evidence for social working memory from a parametric functional MRI study, Proceedings of the National Academy of Sciences, 2012). Thus, SWM and CWM may both rely on the lateral frontoparietal system supporting generic working memory processes, but only SWM may specifically recruit the medial frontoparietal system. Results from Paper 1 are discussed in terms of updating theories of effortful social cognition, medial frontoparietal system function, and implications for clinical populations with dual and/or differential impairments in social cognition and working memory.

To confirm whether there may be a full dissociation in the medial frontoparietal system across SWM and CWM, Paper 2 compared, within a new sample of subjects (N=25), neural responses to the SWM paradigm (thinking about 2, 3, or 4 friends along a trait dimension during a delay period) to a difficulty-matched CWM paradigm (alphabetizing 2, 3, or 4 friends’ names during a delay period). Results showed that the medial frontoparietal system differentially
responds to SWM and CWM: these regions linearly increased as a function of the number of friends considered along trait dimensions in working memory, but linearly decreased as a function of the number of friends’ names alphabetized in working memory. Thus, the medial frontoparietal system may uniquely support SWM processes, despite interfering with CWM processes. Moreover, linear increases as a function of the number of friends considered during SWM in the medial frontoparietal system, but not lateral frontoparietal system associated with generic forms of working memory, predicted individual differences in experimentally measured perspective-taking ability. These results suggest that working memory properties in the medial frontoparietal system track with social cognitive ability and may serve as a useful biomarker for social cognitive ability in clinical populations with deficits in social cognition and perspective-taking, such as schizophrenia, autism spectrum disorder (ASD), and/or social anxiety.

Inspired by these neural results, Paper 3 examines the extent to which, just as CWM training can improve performance on tasks measuring cognitive ability (e.g., math and reading ability; Chein et al., 2010; Holmes et al., 2009), SWM training may improve social cognitive performance, and the extent to which such transfer effects may be unique to SWM (versus CWM) training. 57 participants were randomly assigned to complete SWM or CWM training. Both training interventions improved SWM, as well as perspective-taking performance. Thus, social cognition may be plastic and bolstered by working memory training. However, SWM training (vs. CWM training) uniquely related to the social cognitive gains in perspective-taking. Moreover, individuals with the most autistic traits, an index of social competence, showed the most gains in SWM only if they had undergone SWM (but not CWM) training. Consistent with the brain imaging results from Papers 1 and 2, results from Paper 3 suggest that SWM and CWM training may improve social cognition through at least partially different underlying mechanisms.
Together, these studies suggest that SWM relies on at least partially unique neurocognitive mechanisms than CWM and that these unique mechanisms may be trained to bolster social cognitive ability. Results are discussed in terms of advancing theories of social cognition and working memory, as well understanding the etiology of various clinical disorders associated with social cognitive deficits.
The dissertation of Meghan Leigh Meyer is approved.

Naomi I. Eisenberger
Michael F. Green
Jesse Rissman
Shelley E. Taylor
Matthew D. Lieberman, Chair

University of California, Los Angeles
2014
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First, thank you Matt Lieberman. For the past six years, you have been instrumental in crafting how I conduct and think about research. Perhaps more importantly, you have done so with enthusiasm and kindness. There is no way I could have pulled this off without your intelligent and caring advising. Second, I would like to acknowledge Naomi Eisenberger. I am immensely grateful for our spontaneous advisor-advisee relationship. Thank you for helping me think through my ideas, sharing your own, and being an inspiring model of a contemporary female neuroscientist. Third, thank you Shelley Taylor for supporting the ideas and research on social working memory. I remember timidly presenting these ideas in your lab meeting six years ago, and you gave me the confidence to pursue them full force and helped me get the papers up to snuff for publication. I am grateful to have been able to collaborate with you on this work. I would also like to thank Jesse Rissman, whose feedback on the design of these studies has been crucial to making them as methodologically sound as possible. And thank you Michael Green, your input is critical for translating the ideas behind social working memory to potentially understanding social cognitive deficits in clinical disorders.

Thank you SCN/SAN lab members for your feedback, support, and fun. In particular, I would like to acknowledge Tristen Inagaki, Keely Muscatell, Locke Welborn, Kate Humphreys, Kate Haltom, Jen Regen, and Jared Torre. Thank you all for being my pillars of social support for the past six years. Bob Spunt and Elliot Berkman, thanks for coaching me in fMRI data analysis—you were both incredibly helpful during my training.

Finally, thank you family for your longtime support, care, and love, all of which has helped me complete this work. And Joe, your love, patience, and curiosity helped keep me inspired along this path. In particular, thanks for listening to me talk endlessly about research,
calming me down when I worry about each move in the chess game that is an academic career, and helping me create a social working memory training website! Last, but never least, Dad, thank you not only for your unending love, but also for being my example of a dedicated and egalitarian thinker. Dad, this dissertation is for you.
Vita

Education

2012  Candidate in Philosophy in Psychology, University of California-Los Angeles
2009  Master of Arts in Psychology, University of California-Los Angeles,
2006  Master of Arts in Cognitive Science, École Normale Supérieure
2004  Bachelor of Arts in Psychology, Emory University

Fellowships, Honors, & Awards

2013  International Cultural Neuroscience Consortium (ICNC) Travel Award
2012  Ruth L. Kirschstein NIMH National Research Service Award, Predoctoral Fellow
2012  Harold H. Kelley Award for Best Basic Science Research Paper, UCLA
2012  UCLA Advanced Neuroimaging Summer Training Fellowship
2011  fMRI Training Course Fellowship, University of Michigan
2011, 2009  UCLA Graduate Summer Research Mentorship Fellowship
2010  National Science Foundation East Asian and Pacific Summer Institute Fellowship
2008  UCLA Graduate Fellowship

Publications


**Manuscripts under review:**


**Manuscripts in preparation:**

Meyer, M. L., & Lieberman (in prep). A unique neurocognitive network for social working memory and its link to social cognitive ability.


INTRODUCTION

Successful social interaction requires keeping track of various amounts of social cognitive information on a moment-to-moment basis. Whether keeping track of a handful of friends’ perspectives in a conversation, a roomful of colleagues beliefs during a meeting, or the political ideology of someone we just met, humans often represent, temporarily store and manipulate a great deal of social cognitive information in mind to help them navigate the social world. Indeed, individuals with autism spectrum disorder (ASD), who suffer from social cognitive deficits and poor social interactions, are likely to endorse the statement, “In a social group, I cannot easily keep track of several different people’s conversations,” (Baron-Cohen, 2001). While the ability to juggle multiple pieces of social cognitive information is critical to smoothly navigating the social world, we know next to nothing about how people manage social information in mind. In the present dissertation, I address this gap by suggesting that managing demands to social cognition engages what I term ‘social working memory’ and provide the first empirical evidence showing that social working memory processes rely on partially distinct neurocognitive mechanisms than those supporting non-social forms of working memory.

What is social working memory?

In order to define social working memory, it is critical to address what is meant by ‘working memory’ in psychology. In psychology, working memory refers to the ability to maintain and manipulate information in mind, without the aid of external resources like pen and paper. For example, if while playing a board game like chess, a person were to imagine alternative moves and their consequences, then they would have engaged working memory. Research on working memory began in 1956, when George Miller discovered that humans can store and make use of a limited amount of information in mind (Miller, 1956). For the
subsequent fifty-eight years, psychologists have investigated working memory from many angles. For example, researchers have sought to determine how the mind organizes (or, ‘chunks’) information in working memory (Gobet et al., 2001), which strategies are used to maintain versus manipulate information in working memory (D’Esposito et al., 1999), which neural mechanisms support working memory (e.g., Postle 2006; D’Esposito et al., 1999; Rypma et al., 1999), and how individual differences in working memory processes link to individual differences in general intelligence and reasoning (e.g., Engle et al., 1999; Kyllonen & Christal, 1990), just to name a few. Across these and the many other research directions in working memory, the theoretical concept of working memory consistently refers to the ability to consciously represent, temporarily store, and manipulate information in mind, and the function of working memory is thought to serve as a kind of mental workspace that helps humans link perception, long-term memory and action (e.g., Baddeley, 2003).

In light of the concept of working memory, imagine the following social scenarios: a discussion in which intergroup members must interpret multiple perspectives to resolve a conflict; a business meeting in which employees and bosses keep track of various colleagues’ intentions; a coffee date between friends in which, while one friend vents her troubles, the other friend considers how different pieces of advice may make her friend feel better or worse about her problems. These scenarios are tied by a common theme—people manage in mind a great deal of information about what other people are thinking to meet various social goals, ranging from tolerance, to wise business decisions, to social support. While the process of determining other peoples’ perspectives, intentions, and/or beliefs, a process referred to as ‘mentalizing (Frith & Frith, 2006; Van Overwalle, 2009, 2011),’ is heavily studied in social cognition research, the role of working memory processes in mentalizing has been overlooked. Similarly, prior working
memory research has examined working memory processing for strictly cognitive information (e.g., letters, shapes, numbers) but has not examined working during mentalizing. And yet, if one were to compare the mental steps involved in mentalizing with working memory, they appear to be quite similar. All of the scenarios described above, require the representation, temporary storage, and manipulation of social information in mind.

The parallels between mentalizing and working memory are not limited to these scenarios. For example, the test traditionally used to determine whether or not a person can ‘mentalize,’ called the false-belief task (Premack & Woodruff, 1978), is reminiscent of working memory. In the false-belief task, a participant sees two boxes and another person named Sally who can see the boxes. Sally puts some candy in one of the boxes and leaves the room. The participant next observes an experimenter move the candy to the other box and leave the room. Sally returns to the room and the participant is asked which box Sally believes the candy is in. To pass this test, social cognition researchers suggest, the participant must be able to represent other people’s states of mind because the participant can only derive a correct answer if they appreciate that another person’s state of mind can be unique from their own (e.g., Sally will think the candy is in the box she originally put it in, even though the participant knows that the experimenter moved the candy to a different box). But, defining why someone can pass this test can be cast in another light. That is, it could also be said that passing this test requires the participant to temporarily store, maintain, and manipulate the information about Sally’s state of mind in order to determine which box Sally believes the candy is in. In other words, passing the false-belief task, the traditional index of mentalizing capacity, engages working memory for mental state information.

Building on existing models of working memory, the theoretical perspective put forth in the present dissertation is that ‘social working memory’ refers to the conscious representation,
temporary storage, and manipulation of mental state information. Given the present theoretical perspective that information-processing demands to mental state understanding engage social working memory processes, the primary goals of the dissertation studies here are to determine 1) the basic neurocognitive mechanisms supporting social working memory, 2) isolate whether these mechanisms are similar to or different from those neurocognitive mechanisms supporting previously studied forms of working memory, and 3) the extent to which social working memory may be a useful construct in understanding individual differences in social cognitive ability.

**Translational implications for social working memory research**

Determining the basic mechanisms guiding social working memory is not only important for developing a more complete picture of real-world social cognitive processing, where demands to mental state processing abound, but also for better understanding the etiology of social cognitive deficits in clinical populations. Several clinical disorders (e.g., schizophrenia, ASD, and social anxiety) are associated with either dual or differential deficits in mentalizing and working memory (Amir et al., 2011, Couture et al., 2006; Goldman-Rakic, 1994; Ozonoff et al., 2001; Baron-Cohen et al., 1985), and thus measuring social working memory in these populations may better characterize their social cognitive challenges. Moreover, given recent research finding that working memory training interventions can improve cognitive ability in both healthy and clinical populations (e.g., Jeaggi et al., 2008; Klingberg et al., 2005), social working memory training interventions (such as the one developed for Study 3 here) may likewise improve mentalizing ability in these populations.

**Why has the construct of social working memory been previously overlooked?**

Given the theoretical and translational relevance of social working memory, why has no extent work studied this topic? A critical barrier that likely prevented research on social working
memory in the past is that studies tend to find similar patterns of behavioral performance (accuracy, reaction time) across social and non-social cognitive processing demands (Apperly, 2008; German & Hehman, 2006; Kinderman et al., 1998). Moreover, taxing non-social forms of working memory corresponds with worse performance on challenging social cognitive tasks (Gilbert, 1998), further suggesting that demands to social and non-social cognition share a single pool of working memory resources. The predominant assumption therefore has been that both forms of information processing rely on one working system.

However, two distinct lines of research (that traditionally are not considered in conjunction) question this assumption. On the one hand, research in social neuroscience finds that mentalizing, such as thinking about a person’s mental state and personality, reliably recruits neural activation in a medial frontoparietal system, often referred to as the ‘mentalizing system’ (Kampe et al., 2003; Mitchell et al., 2005; Saxe & Wexler, 2005). Given these findings, it seems reasonable to expect that working memory demands afforded by social cognition would be underpinned by this mentalizing system. On the other hand, research in cognitive neuroscience consistently finds that the mentalizing system linearly decreases in activation during working memory (Greicius et al., 2004; McKiernan et al., 2003). In fact, a failure to decrease the mentalizing system during working memory actually interferes with working memory performance (Anticevic et al., 2010). Working memory instead recruits a lateral frontoparietal network, as these regions linearly increase as a function of working memory load (Rypma et al., 1999). These findings have led to the interpretation that the mentalizing system does not have working memory properties, and instead may actually thwart working memory processes. Importantly, with the exception of studies examining working memory for static face images (e.g., Haxby et al., 1995; Jackson et al., 2008), none of the research in cognitive neuroscience has
manipulated working memory for social cognitive information like mentalizing. Likewise, none of the research in social neuroscience had manipulated the amount of social cognitive information managed in mind during mentalizing. Thus, prior to these dissertation studies, it was unknown how the brain supports working memory processes during mentalizing.

**Goals of the present dissertation**

The goal of the present dissertation was three-fold, with each goal addressed by a unique study. First, given that no prior work had examined social working memory, the first goal was to reveal the neural mechanisms underlying social working memory, with a specific emphasis on how the lateral frontoparietal and mentalizing systems respond during social working memory. The second goal was to isolate which, if any, of the neural mechanisms engaged during social working memory are selective to social working memory, relative to non-social working memory, as well as the extent to which these mechanisms relate to an objective measure of social cognitive ability (i.e., perspective-taking). The third goal of the dissertation was to examine the extent to which social working memory, like cognitive working memory, can be trained and whether social working memory training may improve social cognitive ability (i.e., perspective-taking).

To meet the first goal of determining the neural mechanisms underlying social working memory (Study 1), I developed a novel social working memory paradigm that participants (N=16) completed while undergoing functional magnetic resonance imaging (fMRI). During their scan, participants completed social working memory trials in which they considered 2, 3, or 4 friends along a trait dimension (e.g., funny) during a delay period. A feature of neural systems supporting working memory is that they linearly increase in activity as a function of working
memory load (Rypma et al., 1999). I found that the lateral frontoparietal network previously associated with non-social working memory, and the mentalizing system previously associated with easy forms of social cognitive processing, both linearly increased in activity as a function of social working memory load (i.e., the number of friends considered along a trait dimension). Moreover, only linear increases in the mentalizing system correlated with individual differences in self-reported perspective-taking. Thus, results from Study 1 suggest that social working memory relies on domain-general (lateral frontoparietal) and domain-specific (mentalizing) systems. Moreover, the domain-specific working memory properties in the mentalizing system may help support the working memory demands afforded by everyday social life, such as the need to keep in mind another person’s perspective during social interaction.

Study 2 addressed the second goal of determining the neural mechanisms specific to social working memory, versus non-social working memory, and how they relate to social cognitive ability. Although Study 1 showed that the mentalizing system linearly increased as a function of social working memory load, and this pattern is different from those observed in prior working memory paradigms, in order to confirm a full dissociation in the mentalizing system across the two forms of working memory, I needed to be able to test whether within the same sample of participants, the same mentalizing regions that linearly increase as a function of social working memory load also linearly decrease as a function of non-social working memory load in a similarly formatted, but non-social working memory task. Moreover, to bolster the interpretation from Study 1 that social working memory properties in the mentalizing system relate to individual differences in social cognitive ability, participants’ perspective-taking ability was measured experimentally outside of the scanner.

In Study 2, a new sample of participants (N=25) completed the social working memory
task used in Study 1 (in which they considered 2, 3, or 4 friends’ traits during a delay period) as well as a difficulty-matched non-social, ‘cognitive working memory’ task (in which they alphabetized 2, 3, or 4 friends’ names during a delay period) while undergoing fMRI scanning. Results indeed suggest a full dissociation in the mentalizing system across the two forms of working memory. While the lateral frontoparietal network linearly increased as a function of load for both working memory tasks, the mentalizing system linearly increased as a function of social working memory load, but linearly decreased as a function of non-social working memory load. Moreover, linear increases during social working memory trials in the mentalizing system, but not lateral frontoparietal system, predicted perspective-taking performance. These results complement and extend the interpretations from Study 1: social working memory differentially engages the mentalizing system and working memory properties in the mentalizing system during social working memory predict an objective (rather than self-reported) measure of perspective-taking.

The neural results from Studies 1 and 2 suggested that the mentalizing system might uniquely support social working memory. Study 3 considered this observation in the context of recent findings that working memory training improves non-social working memory capacity (e.g., the number of items that can be dealt with in working memory), as well as performance on other, related cognitive tasks (e.g., math and reading ability; Chein et al., 2010; Holmes et al., 2009). Thus, the third purpose of the dissertation addressed in Study 3 was to examine 1) whether social working memory, like non-social working memory, can be trained and 2) whether training social working memory can improve social cognitive ability. I developed novel, online (Internet website) social working memory training and non-social working memory training interventions based on the tasks used in Studies 1 and 2. Each online training intervention was
computer-adaptive in that trials increased or decreased in difficulty depending on participants’ task performance. Fifty-seven participants were randomly assigned to complete social working memory or non-social working memory training over the internet once/day for 12 days. Social working memory, non-social working memory and perspective-taking performance was measured in the lab pre- and post-training. Both working memory training interventions improved participants’ performance on the two forms of working memory and perspective-taking. However, individuals with worse social competence (measured by the Autism Quotient (Baron-Cohen, 2001)) showed significant improvement after SWM training, but not CWM training. Moreover, improvements in SWM capacity uniquely predicted social cognitive improvements on the perspective-taking task. Together, these results suggest that social working memory, like non-social working memory, can be trained and that training may have transfer effects to other forms of social cognitive ability. Moreover, the results parallel and extend the neural observations from Study 1 and Study 2. Just as social working memory may rely on at least partially unique neural mechanisms, social cognitive improvements via social working memory training may likewise result from plasticity in at least partially unique mechanisms than those trained during non-social working memory.

The three studies of this dissertation are the first to examine the basic mechanisms guiding social working memory, or the ability to manage variable amounts of social cognitive information in mind. It is my hope that these studies not only help carve a more complete picture of how working memory processes may unfold in everyday social life, but also help to launch future translational work examining how social working memory processes may be comprised, and perhaps trained, in various clinical populations who struggle with social cognition, such as schizophrenia, ASD, and social anxiety.
PAPER 1:

Evidence for Social Working Memory from a Parametric Functional MRI Study

(Published in Proceedings of the National Academy of Sciences of the United States of America)
Abstract

Keeping track of varying amounts of social cognitive information, including people’s mental states, traits, and relationships, is fundamental to navigating social interactions. However, to date no research has examined which brain regions support variable amounts of social information processing (social load). We developed a social working memory paradigm to examine the brain networks sensitive to social load. Two networks showed linear increases in activation as a function of increasing social load: the medial frontoparietal regions implicated in social cognition and the lateral frontoparietal system implicated in non-social forms of working memory. Of these networks, only load-dependent medial frontoparietal activity was associated with individual differences in social cognitive ability (trait perspective-taking). While past studies of non-social load have uniformly found medial frontoparietal activity decreases with increasing task demands, the current study demonstrates these regions do support increasing mental effort when such effort engages social cognition. Implications for the etiology of clinical disorders that implicate social functioning and potential interventions are discussed.
Evidence for Social Working Memory from a Parametric Functional MRI Study

The ‘social brain hypothesis’ suggests that the fundamental evolutionary constraint leading to the increase in primate brain size, relative to body size, was the need to keep track of an increasing number of social relationships (Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976). Successful navigation of group living requires not only keeping track of one’s own relationships with others, but also other peoples’ relationships with each other, and the particular characteristics of other people and their relationships. The information to be considered grows exponentially with the number of people considered, making it difficult to think about even a handful of people at once.

Although the online maintenance or manipulation of multiple pieces of social information, or social working memory, is central to successful functioning in a social context, the brain mechanisms guiding this ability remain elusive. One possibility is that increases in social information processing demands are supported by generic working memory resources. Working memory is the psychological process commonly associated with the holding and flexible updating of multiple pieces of information in mind. As people maintain or manipulate increasing amounts of information, a well characterized set of brain regions (lateral frontoparietal regions and supplementary motor area (SMA)) become progressively more active (i.e. parametric increases) (D'Esposito, Postle, Ballard, & Lease, 1999; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Wager & Smith, 2003). Studies of working memory have focused almost exclusively on cognitive or perceptual information (letters, numbers, and object locations) and have not examined social information that might have been critical in successful primate group living (traits, beliefs, relationship characteristics). Given that social thinking
typically includes verbal and visuospatial processing demands, canonical working memory regions may support these basic processes during social working memory.

In addition to recruiting the canonical working memory system, social working memory may also rely on another neurocognitive network to support the processing of increasing social cognitive content. There is a set of brain regions associated with thinking about the mental states or psychological characteristics of other people. This *mentalizing* process reliably recruits activity inmedial frontoparietal regions(279,466),(575,537) and the tempoparietal junction (TPJ; (Kampe, Frith, & Frith, 2003; Mitchell, Neil Macrae, & Banaji, 2005; Saxe & Wexler, 2005)). These regions have been observed in numerous studies pitting a social cognition task (i.e., thinking about people’s psychological characteristics or mental states) against a cognitive control task (i.e., making judgments about physical objects). However to date, no studies have examined whether these regions parametrically increase in activity as the amount of social information maintained or manipulated during mentalizing increases.

Increased activation in mentalizing regions in response to parametric increases in social cognitive effort would counter the current understanding of how the brain responds during effortful cognitive processing. Extant research suggests that the canonical working memory system supports effortful processing, whereas regions in the mentalizing system deactivate during effortful cognition, including during traditional working memory tasks (Greicius & Menon, 2004; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003). Essentially, the relationship between the canonical working memory network and the mentalizing network typically looks like two sides of a seesaw: as the lateral frontoparietal network parametrically increases in activation in response to cognitive effort or task demand, the mentalizing network shows parametric decreases (Greicius & Menon, 2004; McKiernan et al., 2003; Metzak et al.,
In fact, the mentalizing network is virtually identical to a network dubbed the default-mode network (M. Raichle & Snyder, 2007; M. E. Raichle et al., 2001; Spreng, Mar, & Kim, 2009), so named because it is more active when individuals are at rest (i.e. by default) than when they engage in a variety of effortful cognitive tasks.

Given the previously identified dynamics between canonical working memory and mentalizing networks, as well as the mentalizing network’s tendency to show reduced activity under conditions of increasing effort, it would be surprising if the mentalizing network showed load-dependent parametric increases during a social working memory task. The critical caveat is that previous studies have only examined increases in effortful processing with cognitive and perceptual load. None of the studies linking increased effort with decreased activity in the mentalizing network have examined increased effort associated with increased social task demands (social load). Given the importance of managing social information to navigate the social environment, however, it is possible that the canonical working memory and mentalizing systems each support social working memory rather than showing the inverse relationship commonly observed between the systems. The major goal of the current study, therefore, was to examine whether one or both of these networks increase activation during social load.

To examine the neurocognitive systems sensitive to social load level, we developed a novel delayed-response social working memory task that varied working memory load in the social domain on a trial-by-trial basis. During scanning, participants completed trials in which they were presented with the names of two, three, or four of their friends (see Figure 1), mentally ranked their friends along a trait dimension during a delay period, and answered a true/false question about their rank order. Two weeks before the scanning session, we obtained each participant’s ranking of ten friends on each of the trait dimensions we used, allowing accuracy
calculations for each trial. First, we explored which brain regions showed parametric increases in activation with increasing levels of social load. Second, we examined whether any activation during social working memory was related to trait perspective-taking, a correlate of social cognitive ability (Davis, 1983). Given that lateral frontoparietal activity during non-social working memory tasks is related to general fluid intelligence (Conway, Kane, & Engle, 2003; Gray, Chabris, & Braver, 2003), it is possible that a parallel relationship exists between social working memory and social cognitive ability.

**Methods**

*Participants*

Sixteen right-handed, native English-speaking participants (10 females, mean age=20, \(SD=.89\)) were recruited from the UCLA community and paid $60 for their participation. All participants provided written informed consent according to the procedures of the UCLA Institutional Review Board.

*Procedure*

Two weeks prior to the scan, participants completed a trait-rating questionnaire for ten of their close friends. A total of 96 traits were selected from previously rated trait adjectives matched on familiarity, frequency of use, and positive valence (Dumas, Johnson, & Lynch, 2002). For each trait, participants rated how much each of their friends possesses the trait on a 1-100 scale (1 being the least and 100 being the most). These ratings were later used to create social working memory trials (see Materials). On the day of the scan, participants were instructed for each trial to read the list of the friends’ names presented simultaneously on the screen (2, 3, or 4 names; “encoding;” 4 secs) and the trait word subsequently displayed for 1.5 sec once the names were removed (see Figure 1). For the delay period (6 secs), participants were instructed to
think about how much each of the previously shown friends possess the given trait and mentally rank them from most to least in terms of the extent to which each friend possesses the trait (e.g., rank them from most funny to least funny). Finally, participants received a true/false probe question regarding the ranked position of a previously encoded friend. For example, a trial with 3 names (Claire, Kristin, Rebecca) may have shown a probe question such as “second funniest?—Rebecca,” and subjects indicated whether, of the group of friends encoded for that trial, the listed name at the probe question (i.e., Rebecca) was the second funniest of the encoded friends. The ranked position in probe question was randomized across trials to avoid mental set effects. Prior to the scan, participants completed practice social working memory trials (distinct from those used in the scans) to become familiar with the task. In the scan, participants completed four runs of the social working memory task. Each run had 24 unique trials presented with jittered crosshair fixation periods between and within trial elements. Between each trial, and between each modeled working memory phase (encoding, delay, retrieval), participants saw a fixation-cross hair presented for a jittered amount of time (jitter time was randomly chosen and centered around a mean of 1.5 secs (Wager & Nichols, 2003)). After the scan, participants completed the Empathy Interpersonal Reactivity Index (Empathy IRI; Davis, 1983).

Materials

For each social working memory trial participants encoded the names of two, three, or four friends selected from a list of their ten close friends that they provided two weeks prior to the scan. In order to control for rating distance effects on task difficulty, we aimed to select friends that were ranked no more than 25 points apart (on the 100 point scale) and no closer than 5 points apart from one another for each trait word. These distances served as a rule for friend name selection and were adhered to as closely as possible given the distribution of ratings given
by the participants (\(M\) distance for friend names within a trial=11.38, \(SD=7.24\)). Each participant was shown their own friends’ names on each trial. Trials were standardized on brightness, contrast, font, and size.

Perspective-taking ability was measured using the perspective-taking (PT) sub-scale of the Empathy IRI (Davis, 1983). This sub-scale was used because we wanted an individual difference measure of social cognition that shows variability in scores across healthy adults. The PT scale is a valid and reliable measure of the tendency to adopt the point of view of other people in everyday life (Davis, 1983). A sample item from the PT scale is “I sometimes try to understand my friends better by imagining how things look from their perspective.” Perspective-taking ability is a fundamental component of social cognition, and higher perspective-taking scores on the Empathy IRI are associated with better social functioning (Davis, 1983).

**Behavioral Data Acquisition and Analysis**

Working memory is thought to be a limited capacity, given that behavioral performance on working memory tasks worsens as a function of load. During our social working memory scanner trials we collected participants’ reaction time to the probe question as an index of task performance. To compute trial accuracy, we compared participants’ answer to the probe question to their original friend trait ratings. If their answer was consistent with their pre-scanner ratings about their friends’ traits, the trial was scored as accurate. For example, on the pre-scan rating questionnaire, for the trait ‘funny’ a subject may have rated Claire an 85, Kristin a 75, and Rebecca a 67. For a trial in which these three friends were encoded, and the probe question was “Second funniest—Rebecca?,” a correct answer would be ‘false’ because Rebecca was actually rated third funniest.
**fMRI Data Acquisition and Analysis**

Imaging data were collected on a Siemens Trio 3-Tesla MRI scanner at the UCLA Ahmanson-Lovelace Brain Mapping Center. For each participant, we acquired 720 functional T2*weighted echoplanar image volumes (EPIs; slice thickness=4 mm (no gap), 34 slices, TR=2000 ms, TE=30 ms, flip angle=90°, matrix=64 x 64, FOV=192 mm) divided evenly across four runs. We also acquired a T2-weighted matched-bandwidth anatomical scan (same parameters as EPIs, except: TR=5000 ms, TE=34 ms, flip angle=90°, matrix=128 x 128).

Imaging data were analyzed in SPM8 (Wellcome Department of Cognitive Neurology, Institute for Neurology, London, UK). Preprocessing for each participant's images included skull-stripping using Brain Extraction Tool (BET) (S. M. Smith, 2002), spatial realignment to correct for head motion, normalization into a standard stereotactic space as defined by the Montreal Neurological Institute, and spatial smoothing using an 8mm Gaussian kernel, full width at half maximum.

The data was modeled as an event-related design. Each trial comprised separately modeled events for encoding (names), delay (6 sec crosshair fixation) and retrieval (probe question about an encoded friends’ trait ranking). Based on previous working memory research (Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster, 1973; Huijbers, Pennartz, Rubin, & Daselaar, 2011; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Rosenkilde, Bauer, & Fuster, 1981; Watanabe, 1986), our fMRI analyses focused only on trials answered correctly at retrieval. Encoding and delay periods were modeled as a boxcar spanning their duration. Retrieval was modeled as a boxcar from probe onset to the subject’s response. Each event type (encoding, delay, and retrieval) also had an associated parametric modulator (regressor) coding for the trial load (2 names, 3 names, or 4 names). We orthogonalized the social load parameter
with respect to the main effect to examine the unique effect of social load, over and above any
effects of performing the task collapsing across load level. We also created a model in which we
orthogonalized the social load parameter with respect to the average effect and any effect
attributable to RT (see results).

For all analyses, linear contrasts were computed for each participant as a measure of
differential BOLD activation, and then entered into random effects analyses at the group level
for statistical inference. All whole-brain analyses were conducted using a statistical criterion of
at least 43 contiguous voxels exceeding a voxel-wise threshold of \( p < .005 \). This joint voxelwise
and cluster-size threshold corresponds to a false-positive discovery rate of 5% across the whole
brain as estimated by a Monte Carlo simulation implemented using AlphaSim in AFNI (Cox,
1996). For visual presentation, thresholded \( t \)-statistic maps were surface rendered using the SPM

Results

Behavioral Task Performance

The purpose of the behavioral analyses was to determine whether our social working
memory task produced characteristic accuracy and reaction time (RT) effects observed in prior
working memory studies. Replicating previous research suggesting that performance decreases
as a function of task demand (working memory load), repeated-measures ANOVA showed a
significant effect of task demand on RT (\( F(2,15)=11.48, p<.001 \)) and accuracy (\( F(2, 15)=5.94, \)
\( p<.005 \)). For RT, post-hoc t-tests revealed RT was significantly longer for 4 names compared to
3 names (\( t(15)=2.45, p<.05; \) Supplementary Table 1) and 2 names (\( t(15)=3.85, p<.005 \)).
Similarly, RT was marginally longer for 3 names compared to 2 names (\( t(15)=1.77, p=.096 \)).
Accuracy was significantly higher on 2 name trials than 3 name trials (\( t(15)=3.04, p<.01 \)) or 4
name trials \((t(15)=3.34, p<.005)\). However, the difference in accuracy for 3 name trials compared to 4 name trials was not significant \((t(15)=.27, p=.79)\).

**fMRI Results**

*Parametric effects during delay.* Parametric analysis of fMRI data allows us to see which regions show a linear increase in activity as a function of social load (i.e., trials with two, three, or four friends’ names to be considered along a trait dimension). Our first analyses focused on the delay period beginning after the trait word (e.g., ‘funny’) was removed until the probe question appeared 6 seconds later (e.g., ‘second funniest?’). In this statistical model, the first regressor (i.e. average effect) codes the fixed amplitude effect (i.e., the average hemodynamic response, collapsing across all levels of load). The second regressor is the parametric effect, which codes the variable amplitude effect, (i.e., the effect of the hemodynamic response that varies by social load). Thus, effects associated with the parametric load regressor are independent of the basic effects associated with performing a social cognitive task, per se.

As expected, parametric analyses showed load-dependent increases in canonical working memory regions including dorsolateral prefrontal cortex (DLPFC: -45, 17, 28), superior parietal lobule (SPL: 30, -67, 58), and SMA (-9, 14, 55). However, in contrast to previous non-social studies of working memory, we also observed load-dependent increases in mentalizing regions including dorsomedial prefrontal cortex extending into anterior paracingulate cortex (DMPFC: -12, 38, 49; DMPFC/APC 12, 29, 31), precuneus/posterior cingulate cortex (PC/PCC: 0, -61, 46) and tempoparietal junction (TPJ: -42, -70, 40; Figure 2, Supplemental Table 2).

*Parametric effects during probe response.* Past working memory studies examine neural responses during the probe response in addition to the delay period, as both are considered component processes of working memory (Rypma & D'Esposito, 1999). Moreover, the probe
response period most closely matches extant social cognitive neuroscience paradigms that do not manipulate social load (i.e., participants make a judgment about others’ traits (Mitchell, Heatherton, & Macrae, 2002)). Therefore, we also modeled activation from the onset of the probe question until participants’ button press to determine which regions would show parametric increases as a function of social load. To examine social load effects during the probe response period, a parametric load regressor was entered for each trial to scale the hemodynamic responses expected during the probe period.

As expected, parametric analysis during the probe response period in canonical working memory regions including DLPFC (-39, 5, 58), SPL (57 -58 40), and SMA (-6, 20, 64). However, we once again also observed load dependent increases in mentalizing regions including DMPFC extending into anterior paracingulate cortex (9, 47, 52), medial prefrontal cortex (MPFC: -6 56 -5), PC/PCC (0, -61, 34) and TPJ (-48, -67, 43; Figure 3, Supplemental Table 2). As with the delay results, these effects were independent of the average effect associated with performing a social task, per se.

Because there were significant differences in the reaction times as a function of social load level, we conducted an additional analysis that added the reaction time for each trial as a parametric regressor. We orthogonalized the social load parameter with respect to the RT parameter to examine the unique effect of social load, over and above any effects of RT and the average effect of performing a social cognition task per se. In this analysis, mentalizing regions (DMPFC, MPFC, PC/PCC, and TPJ) and traditional working memory regions (DLPFC, SMA and SPL) continued to produce activity associated with social load level, independent of reaction time.
Perspective-taking ability. Paralleling findings on non-social working memory and fluid intelligence, we examined whether there was a relationship between the parametric recruitment of regions as a function of social load and a measure of trait perspective-taking ability, which has previously been linked to social competence and social reasoning (Davis, 1983; Underwood & Moore, 1982). A relation between these assessments would provide further validation of the idea that the brain’s ability to manage increasing amounts of social information corresponds with social cognitive ability. Moreover, if the mentalizing regions result in this analysis, it would suggest that social competence depends on brain regions distinct from those commonly associated with general intelligence. Results from the whole-brain regression of the parametric analysis of the delay period with perspective-taking scale scores entered as a regressor showed significant activation in MPFC (-6, 62, 1) and PC (-9, -49, 13) regions, both of which are central to social cognition (Figure 4, Supplementary Table 3). In contrast, perspective-taking did not correlate with parametric activity in any traditional working memory regions.

Discussion

Social load, default-mode, and effort

We identified brain regions involved in maintaining and manipulating increasing amounts of social information that may allow humans to understand complex, multi-faceted social interactions. As expected, the canonical working memory system in lateral frontoparietal regions and SMA produced increased activation during delay and probe response periods as social load increased. Similarly, the mentalizing network in medial frontoparietal regions and TPJ also produced increased activation during delay and probe response periods as social load increased. Finally, only mentalizing regions’ parametric increases correlated with trait differences in perspective-taking ability. Prior meta-analyses of non-social working memory do not report
mentalizing regions increasing with load (6); on the contrary these regions are typically shown to reduce activation as a function of load in non-social working memory tasks (McKiernan et al., 2003; Metzak et al., 2011).

These results are important in part because they identify regions that are not only involved in supporting social cognition generally, but regions that are sensitive to the amount of effort needed to support social cognitive processes. That is, this parametric effect cannot be explained simply by the fact that participants are performing a task with social content. The average effect, collapsing across levels of social load, is also included in the model and thus the parametric regressor captures variability in the neural response over and above that which is explained by the average effect. Countless social psychological phenomena have been understood in terms of effortful versus non-effortful social cognition (Chaiken & Trope, 1999), and some studies have suggested that different systems subserve these kinds of processes (Evans, 2008; Lieberman, Gaunt, Gilbert, & Trope, 2002; E. Smith & DeCoster, 2000; Strack & Deutsch, 2004). Here we report the first neurocognitive evidence of brain regions whose activity scales linearly with increasing task difficulty within the social domain. Furthermore, perspective-taking ability was associated with these load-dependent effects in mentalizing regions, demonstrating that significant variance associated with social cognitive constructs may be explained in part by how the mentalizing network scales its response to the level of social load.

The load-dependent increases in the mentalizing network are also compelling because they run counter to the common finding of parametric decreases in these regions as a function of load level (i.e., during effortful processing). Previous studies have uniformly found that increasing levels of cognitive load in working memory and other related tasks produces load-
dependent decreases in the default-mode network that is essentially identical to the mentalizing network (Greicius & Menon, 2004; McKiernan et al., 2003; Metzak et al., 2011). Given past findings, it would have been reasonable to question whether previous mentalizing effects were partly artifacts of lower task difficulty compared to the non-social control tasks. As noted earlier, the critical caveat to past load-related findings is that they were all derived from tasks using non-social forms of load. The current study suggests that load effects within the mentalizing network are domain-specific and that regions within this network are capable of supporting increasingly effortful cognition, if it is social cognition.

It is also worth noting that in our highest load condition, nearly all of the regions within the mentalizing/default network that were observed to increase parametrically were also significantly more active compared to a resting baseline (Figs 2 and 3). In common social cognition and self-reference paradigms, regions within the mentalizing and default mode network show increased activity compared to a non-social control task (i.e., judgments about the physical world); however they typically show decreased or no activity compared to a resting baseline. Therefore, it is difficult to claim that regions are optimized for social cognition when the tasks used to assess social cognition produce less activity than what is observed during rest. The current data suggest that these prior findings might be due to the lower difficulty levels of prior social cognition and self-reference tasks. When performance measures are reported in fMRI studies of social cognition, they are often near ceiling (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Fletcher et al., 1995; Walter et al., 2004), implying relative ease. In contrast, average accuracy in our most difficult condition dropped below 60%. Our results thus reaffirm the role of these regions in social cognition and suggest the possibility that during rest, individuals are engaged in more complex or challenging kinds of social cognition than what is
demanded by most fMRI studies of social cognition. This seems quite reasonable given that five year olds can pass many of the fMRI-based social cognition tasks given to adults (Sommer et al., 2007; Wimmer & Perner, 1983a), and self-reference tasks involve simple global judgments (‘are you talkative?’) (Kelley et al., 2002).

Importantly, parametric increases in the medial frontoparietal and TPJ regions compliment and extend past research implicating these regions in mentalizing. Previous findings show this network reliably engages when participants think about the mental states, traits, and beliefs of others (Kampe et al., 2003; Mitchell, Neil Macrae, et al., 2005; Saxe & Wexler, 2005); however the operating characteristics of these computations have not been addressed. Our results indicate that at least some components of the mentalizing network are capacity limited and increase activity with effort and social load level. Such findings simultaneously inform and create new hypotheses for research in social neuroscience, as well as research on the default-mode system, which previously characterized this network as interfering with, rather than supporting, effortful cognition (McKiernan et al., 2003; Metzak et al., 2011).

**Social working memory and social cognitive ability**

Although there is no agreed upon measure of social cognitive ability, trait perspective-taking has been associated with social competence (Davis, 1983; Underwood & Moore, 1982). We examined whether perspective-taking was related to load-dependent neural activity during the social working memory task and found that only regions within the mentalizing network showed this effect. Specifically, individuals higher in trait perspective-taking were more likely to show load-dependent parametric increases in MPFC (Brodmann area 10). This is the only region of the frontal cortex known to be disproportionately larger in humans than other primates after scaling for body size (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001).
addition, individual differences in MPFC size correlate with social cognitive competence and social network size (Lewis, Rezaie, Browne, Roberts, & Dunbar, 2011; Powell, Lewis, Dunbar, García-Fiñana, & Roberts, 2010). Our functional finding and the previous structural findings dovetail nicely with the social brain hypothesis, which emphasizes that social load processing may have been critical in the expansion of prefrontal cortex size in humans.

Assessing psychopathology, improving daily functioning

Many psychiatric conditions including schizophrenia, social anxiety, and autism spectrum disorder show dual or differential deficits in social cognition and working memory. Understanding how the medial and lateral frontoparietal networks contribute to social working memory may offer important insights into how these systems contribute to various psychological disorders and the kinds of interventions that might benefit them. For example, both working memory and theory of mind (i.e., the ability to represent other people’s mental states) are impaired in patients with schizophrenia (Couture, Penn, & Roberts, 2006; Goldman-Rakic, 1994; Pickup & Frith, 2001). Individuals with social anxiety show working memory deficits, but enhanced working memory for socially salient words (Amir & Bomyea, 2011). Similarly, a hallmark of autism spectrum disorder is the impaired ability to relate to and take the perspective of others (Baron-Cohen, Leslie, & Frith, 1985; Dawson & Fernald, 1987). Interestingly, research on working memory capacity in individuals with autism spectrum disorder is mixed (Bennetto, Pennington, & Rogers, 1996; Ozonoff & Strayer, 2001; Russell, Jarrold, & Henry, 1996; Williams, Goldstein, & Minshew, 2006), with some research finding that working memory capacity is relatively intact in high-functioning individuals (Bennetto et al., 1996; Ozonoff & Strayer, 2001). It is possible that social cognitive deficits in these and other disorders may be better characterized with the inclusion of a social cognition task like social working memory that
varies in difficulty level.

Social working memory capacity may also explain variance in healthy individuals’ social cognitive abilities. Traditional working memory capacity and lateral frontoparietal activity has been linked to cognitive abilities ranging from math and reading to IQ (Conway et al., 2003; Daneman & Carpenter, 1980; Geary, Hoard, Byrd-Craven, & DeSoto, 2004; Gray et al., 2003). Given that medial frontoparietal activity during our social working memory task was linked to trait perspective-taking, a core social cognitive ability (32), social working memory capacity may be a useful construct for exploring social cognitive ability.

Along these lines, it is also plausible that social working memory training could benefit everyday social competence. Studies show that working memory training not only improves working memory, but these improvements generalize to improved cognitive reasoning and fluid intelligence (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; Jaeggi, Buschkuehl, Jonides, & Shah, 2011; Klingberg et al., 2005). For example, Jaeggi et al. (Jaeggi et al., 2008) found that in psychologically healthy adults with normal IQ, working memory training led to improvements in fluid intelligence, the ability to reason and solve new problems independent of previously acquired knowledge. Similarly, it is possible that social working memory training would improve both social working memory ability (i.e., how many people can someone effectively think about at once) and other forms of social cognitive reasoning (i.e., perspective-taking) in both atypical and typical populations.

**Limitations**

There are a few potential limitations of our study. First, inclusion of a non-social working memory task would allow comparison of activation during social working memory trials to activation during cognitive working memory trials, which could identify activations unique to
social (rather than non-social) working memory. Importantly, this limitation does not detract from our inferences from the current data. That is, our goal was to identify what regions are generally active during social working memory, and in particular, how the medial frontoparietal regions previously associated with decreases during increased mental effort would respond to social cognitive task demand. The responses of both lateral and medial frontoparietal networks across load levels during cognitive working memory have been very clearly characterized in multiple past studies (McKiernan et al., 2003; Metzak et al., 2011). A cognitive comparison therefore would not change the pattern observed here in medial frontoparietal regions, which is qualitatively different than what has been observed in cognitive working memory paradigms in the past.

A second potential limitation is that our task induces both maintenance and manipulation during the delay period, and hence these component processes cannot be teasing apart in our analysis of the delay period. Past research tends to find similar, but more robust patterns of brain activation for manipulation relative to maintenance (D'Esposito et al., 1999; Veltman, Rombouts, & Dolan, 2003) in non-social working memory tasks. Future research will be necessary to identify whether the same trend is true for activation during social working memory maintenance and manipulation.

Conclusions

Gordon Bower (Bower, 1975), a leading memory researcher, once suggested that the purpose of working memory “is to build up and maintain an internal model of the immediate environment and what has been happening in our world.” (p. 54). Past working memory research has focused on the basic building blocks that allow us to handle representations of our immediate environment, but has neglected to incorporate relevant social information that makes up much of
our mental processing. Our results demonstrate that humans possess mechanisms to support social working memory, and that these mechanisms include mentalizing regions in addition to canonical working memory regions. Echoing Bower, we suggest that the purpose of social working memory is to build up and maintain an internal model of the immediate social environment and what has been happening in our social world.
Figure 1. Social working memory task
Figure 2. Parametric increases in the mentalizing and canonical working memory regions during the delay period as a function of social load level. DMPFC=dorsomedial prefrontal cortex; SMA=supplementary motor area; PC/PCC=precuneus/posterior cingulate cortex; DLPFC=dorsolateral prefrontal cortex; TPJ=tempoparietal junciton.
Figure 3. Parametric increases in the mentalizing and canonical working memory regions during the probe response period as a function of social load level. MPFC=medial prefrontal cortex
Figure 4. Regions showing social load dependent increases during the delay period of social working memory trials that correlate with trait-level perspective-taking ability. Top medial view of the brain shows regions in the mentalizing and default-mode network whose parametric activation correlates with perspective-taking scores. This correlation is plotted for MPFC parametric increases by load as a function of perspective-taking scores. The bottom lateral view of the brain shows that none of the regions in the frontoparietal canonical working memory network showed parametric activation correlating with perspective-taking scores.

PCC=posterior cingulated cortex.
References


PAPER 2:

A unique neurocognitive network for social working memory and its link to social cognitive ability
Abstract

The social world is incredibly complex and the ability to manage social information in mind is critical for success as a social species. Typically, it has been assumed that social cognitive demands generated by the social world are managed by generic working memory mechanisms designed to maintain and manipulate information on a moment-to-moment basis. In the present study, it was found that SWM differentially engages a medial frontoparietal system associated with thinking about minds. This ‘mentalizing system’ linearly increased as a function of SWM load (the number of friends considered along trait dimensions during a delay period), but decreased as a function of CWM load (alphabetizing friends’ names during a delay period). Moreover, linear increases in the mentalizing system, but not the lateral frontoparietal system associated with generic forms of working memory, predicted performance on an objective measure of perspective-taking ability. These findings suggest that the mentalizing system may uniquely support SWM and that working memory demands afforded by challenging social cognition, such as the need to manage another person’s perspective in mind, may be underpinned by this mentalizing system.
A Unique Neurocognitive Network for Social Working Memory and its Link to Social Cognitive Ability

“The best mechanic in the factory may fail as a foreman for lack of social intelligence.”
Edward L. Thorndike

The capacity to reason, generate solutions to problems, and innovate sets humans apart from other primates. Yet, as the quote from Thorndike notes, cognitive intelligence alone is insufficient for human success. In addition to the ability to think intelligently about cognitive information—such as spatial reasoning and logic—humans must be able to think intelligently about people’s states of mind—their perspectives, traits, and intentions—to guarantee survival in a social world. For centuries, a dominant view has been that the capacity to understand minds is one of many examples of a general human ability to reason and think abstractly (Goleman, 2007). However, if this were the case, it is unlikely that humans with the greatest cognitive capacities could fall short of social intelligence. Yet, as Thorndike observed, cognitive and social intelligence do not necessarily align within the same individual.

A critical component of intelligent thought is working memory, the ability to maintain and manipulate information in mind, without the aid of external resources, such as pen and paper (Andrade, 2001; Miller, 1956; Miyake & Shah, 1999). We recently showed (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012) that social working memory (SWM), or the ability to maintain and manipulate social cognitive information, recruits two distinct neurocognitive networks, the lateral frontoparietal system associated with traditional cognitive working memory (CWM) tasks (D'Esposito et al., 1999; Rypma et al., 1999; Wager & Smith, 2003) and general intelligence (Duncan, Burgess, & Emslie, 1995; Hampshire, Thompson, Duncan, & Owen, 2011), and the medial frontoparietal system, often termed the mentalizing system (Frith & Frith,
2006), associated with mental state reasoning (Kampe et al., 2003; Mitchell, Banaji, & Macrae, 2005; Saxe & Wexler, 2005). Importantly, both networks showed a linear increase in activation as a function of SWM load (i.e., the number of friends considered along a trait dimension during SWM), which is a response pattern characteristic of working memory systems (Rypma et al., 1999). Moreover, linear increases in activation as a function of SWM load in the mentalizing system, but not the lateral frontoparietal system, were associated with individual differences in self-reported perspective-taking, a hallmark of social cognitive ability (Davis, 1983). Thus, while SWM may recruit both the lateral frontoparietal system and the mentalizing system, it is possible that only the mentalizing system is specialized for SWM, and that the ability to linearly increase this network in response to increases in SWM load uniquely relates to social cognitive ability.

Two critical issues, however, limit this interpretation. First, to confirm a specialized role for the mentalizing system in SWM, linear responses in the mentalizing system must differentiate between manipulations of SWM load and cognitive working memory (CWM) load within the same sample of participants. The original SWM study employed a parametric modulation design in which SWM load varied on a trial-by-trial basis. In this design, each lower working memory load level serves as a control condition for the subsequently higher working memory load level. That is, a brain region’s activity is linearly associated with SWM if it increases when considering three-relative-to-two and four-relative-to-three people along trait dimensions in SWM. While this analysis isolates all neural regions associated with SWM, it does not specify which neural regions are specific to SWM, relative to CWM.

Second, if the ability to parametrically recruit the mentalizing system as a function of SWM load is critical to social intelligence, then linear increases in activation in the mentalizing system as a function of SWM load should predict objective measures of social cognitive ability.
Although we have shown that greater self-reported perspective-taking is associated with linear increases in mentalizing system activation during SWM (Meyer et al., 2012), interpretations from self-reported skills are limited (e.g., (Nisbett & Wilson, 1977)). A more valid analysis would be to show that individual differences in linear increases in the mentalizing system, and not the lateral frontoparietal system, during SWM predict an objective measure of perspective-taking skills.

The current study was designed to address these limitations and clarify the neural mechanisms that are unique to SWM, as well as the neural mechanisms that uniquely tie SWM to social cognitive ability. While undergoing fMRI scanning, participants completed SWM and CWM delayed match-to-sample tasks that were identical in format except for the working memory process engaged during the delay period. For the SWM task, participants ranked their friends along trait dimensions during a delay period, whereas during the CWM task, participants alphabetized their friends’ names during a delay period. After their scan, participants completed a computerized task (i.e., a variant of the Director’s task (Dumontheil, Küster, Apperly, & Blakemore, 2010; Keysar, Barr, Balin, & Brauner, 2000) designed to measure perspective-taking ability.

Methods

Participants

Twenty-five right-handed participants (15 female, mean age=21.56, SD=2.5) from the University of California, Los Angeles (UCLA) community participated in this study. Participants were paid $100 and provided written informed consent according to the procedures of the UCLA Institutional Review Board.

Procedure
As in the original SWM study (Meyer et al., 2012), participants completed the friend trait-rating questionnaire for ten of their close friends two weeks prior to scanning. For each trait, participants rated how much each of their friends possesses the trait on a 1-100 scale (1 being the least and 100 being the most). These ratings were later used to create SWM trials (see Materials). During their scan, participants completed SWM trials in which they encoded two, three, or four of their friends’ names, ranked the friends along a trait dimension during the delay period, and answered a true/false question about their rank order (Figure 1). Additionally, participants completed CWM trials in which they alphabetized their friends’ names during the delay period (Figure 1). To keep the format between SWM and CWM trial types as similar as possible, for the true/false question, participants read a ranked position and a friend’s name with a question mark (e.g., second: Claire?) and determined if the position was true or false based on their ranking. Thus, SWM and CWM trials only differed in terms of the instruction word shown prior to the delay period. Prior to their scan, participants completed practice SWM and CWM trials (distinct from those shown during the scan) to become familiar with the task. Participants were instructed to answer questions as quickly and accurately as possible and used a button-box in the scanner to record their answers to the true/false questions for each trial.

In the scanner, participants completed a structural scan (MP-RAGE) and 3 functional scans. Each functional scan included 18 SWM trials (6 trials in which two friends were encoded, 6 trials in which three friends were encoded, and 6 trials in which four friends were encoded) and 18 CWM trials (6 trials in which two friends were encoded, 6 trials in which three friends were encoded, and 6 trials in which four friends were encoded). The 18 trials of each working memory type were presented in blocks of 9 trials, with the cue ‘traits’ or ‘alphabetize’ shown prior to each block to ensure that participants knew which trial type they were going to complete next. The
order of these blocks was counterbalanced across participants. Trials within each block were jittered in timing (within and between trial elements) and ordered according to Optimize Design (Wager & Nichols, 2003).

After their scan, participants completed the Director’s Task ((Dumontheil et al., 2010; Keysar et al., 2000); Figure 2), a computerized, objective measure of perspective-taking ability, in a quiet testing room outside of the scanner. In this task, participants observe a bookshelf with various objects and a woman by the bookshelf (the ‘Director’) asks the participant to move one of the objects that appears on the shelf. Some of the shelves on the bookshelf have a wall behind them and others do not. Importantly, for half of the trials (8 trials total), the director has the same perspective as the participant and can see all of the objects on the bookshelf (first-person perspective condition). For the other half of the trials (8 trials total), the director is standing on the other side of the bookshelf and therefore cannot see the items on the shelf that are blocked by the shelf walls (third-person perspective condition). For both trial types, the Director asks for one of three objects of the same category to be moved up, down, or to the side. For example, for a trial in which there are three cameras on the bookshelf as well as other various objects, the director may ask to move the top camera down. Thus, the degree of cognitive information processing is identical for both trial types except for the need to adopt the director’s perspective for the third-person perspective condition. For each trial, one of the three objects pertinent to the director’s request was blocked by a shelf wall, ensuring the necessity of perspective-taking to determine a correct answer in the third-person perspective trials. To avoid mental set effects, all trials showed different objects on the bookshelf, the shelves that were blocked by walls varied from trial to trial, and additional trials (8 additional trials total), in which directors ask the participant to move one object not belonging to a set of objects (e.g., move the popcorn to the
side) were included. These latter trials were not included in the analyses because they less clearly isolate perspective-taking. That is, participants can correctly answer third-person perspective trials with strategies other than perspective-taking when they are not required to assess which of three objects the director wants to be moved. For each trial, first the participant heard via an audio recording the director ask for an object to be moved (2.5 seconds) and next an arrow appeared on the screen indicating one of the objects to be moved. When the arrow appeared on the screen, participants indicated by keyboard button press whether the arrow that appeared on the screen corresponded with the object that the director asked to be moved. Participants had up to 5 seconds to make their response after which the screen advanced to the next trial.

**Materials**

For each SWM trial, participants encoded the names of 2, 3, or 4 friends selected from a list of their 10 close friends that they provided 2 weeks before the scan. Consistent with the original SWM study (Meyer et al., 2012), to control for rating distance effects on task difficulty, we aimed to select friends that were ranked no more than 25 points apart (on the 100-point scale) and no closer than 5 points apart from one another for each trait word. These distances served as a rule for friend name selection and were adhered to as closely as possible given the distribution of ratings given by the participants (Mean distance for friend names within a trial=12.60; SD=4.00). Each participant was shown their own friends’ names on each trial. For both the SWM task and the Director’s task performed outside the scanner, trials were standardized on brightness, contrast, font, and size.

**fMRI Image Acquisition**

Functional images were acquired on a 3 Tesla (T) Siemens Trio with a T2*-weighted echo-planar plus sequence covering 36 axial slices (TR/TE=2000/25 ms, flip angle=90 degrees,
64 x 64 matrix, 3mm 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 x 256 matrix, 1mm thick, 192 sagittal slices, FOV=256).

**Data Analysis**

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 (3mm isotropic) and applied spatial smoothing (Gaussian kernel of 8mm, full width at half maximum).

At the first level of analysis, each participant’s preprocessed data was modeled as an event-related design in the general linear model framework. Thus, we modeled regressors for each trial component (encoding, delay, retrieval) separately for SWM and CWM trials and regressors of no interest capturing the portions of the task not related to trials, as well as 6 motion regressors for each of the motion parameters from image realignment. Encoding and delay periods were modeled as a boxcar spanning their duration. Retrieval was modeled as a boxcar from probe onset to the participant’s response. Each event type (encoding, delay, and retrieval) also had an associated parametric modulator (regressor) coding for the trial load (2 names, 3 names, or 4 names). We orthogonalized the social load and cognitive load parameters
with respect to the main effect of each working memory type to examine the unique effect of social load vs. cognitive load, over and above any effects of performing the tasks collapsing across load level.

At the second level of analysis, the linear contrasts computed for each participant as a measure of differential BOLD activation were entered into random effects analyses at the group level for statistical inference. All whole-brain analyses were conducted using a statistical criterion of at least 39 contiguous voxels exceeding a voxel-wise threshold of \( p < .005 \). This joint voxelwise and cluster-size threshold corresponds to a false-positive discovery rate of 5% across the whole brain as estimated by a Monte Carlo simulation implemented using AlphaSim in AFNI (Cox, 1996). For visual presentation, thresholded \( t \)-statistic maps were surface rendered using the SPM Surfernd toolbox Version 1.0.2 (I. Kahn; http://spmsurfernd.sourceforge.net).

We performed the following second level analyses on delay period activation to examine our questions regarding SWM. First, to examine the neural processes common to SWM and CWM, we performed whole-brain conjunction analysis, using a factorial repeated-measures ANOVA (within subject factor: parametric modulator coding working memory load; blocking factor: subject) to test the conjunction null (Nichols, Brett, Andersson, Wager, & Poline, 2005) of parametric modulation by SWM load level and CWM load level. Second, to identify neural activity specific to SWM, we performed whole-brain analysis contrasting parametric modulation by load for SWM versus CWM trials. Third, to examine whether parametric recruitment of the mentalizing system as a function of SWM load uniquely predicts perspective-taking ability, we performed linear regression. For each participant, average parametric modulation of activation as a function of SWM load versus CWM load in the clusters observed in the whole-brain contrast was computed and then used as a predictor variable in a linear regression model predicting
perspective-taking ability. To isolate perspective-taking ability, the dependent variable was accuracy on third-person perspective trials, controlling for accuracy on first-person perspective trials (i.e., the unstandardized residuals resulting from the regression of first-person perspective accuracy on third-person perspective accuracy).

Results

Behavioral Results

Before examining neural effects across the two forms of working memory, it is important to ensure that any observed neural differences do not reflect differences in task difficulty, rather than differences in working memory mechanisms. Thus, we performed a 2 (SWM versus CWM) X 3 (load level: 2 friends, 3 friends, 4 friends) repeated-measures ANOVA on participants’ mean reaction times (RTs). Results showed that reaction times for each load level across the SWM and CWM trials were not statistically different ($F(2, 24)=1.25, p=.3$, Figure 3). Each working memory task showed significant increases in RT as a function of load, however, suggesting the more friends considered during each working memory task, the greater demands to SWM or CWM, respectively (SWM $F(2, 24)=62.80, p<.0001$; CWM $F(2, 24)=41.21, p<.0001$). Each post-hoc comparison between working memory load level, separately for SWM and CWM trials, was significant ($ps<.005$), suggesting each load level significantly increased working memory demands.

Consistent with the idea that the social cognitive processing demands afforded by third-person perspective-taking trials make them more challenging than the first-person perspective-taking trials, participants were significantly slower to respond and marginally less accurate in their responses for the third-person perspective trials than first-person perspective trials (Mean RT third-person perspective=1.36 secs, Mean RT first-person perspective=1.24 secs, $t(24)=2.14$, $p<.05$).
Mean accuracy first-person perspective = 86%, Mean accuracy third-person perspective = 81\% \quad t(24) = 1.59, p = .14). RT and accuracy on the director’s task did not significantly correlate for either the first-person perspective or third-person perspective trials (ps > .65), thus only accuracy was used as a measure of perspective-taking performance. That is, because reaction times for the third-person perspective trials did not correlate with accuracy, faster reaction times, across our sample of participants, could reflect some combination of a failure to adopt the Director’s perspective or more easily adopting the Director’s perspective. Thus, only accuracy was used as an index of perspective-taking ability.

**Neural Results**

**Whole-Brain Analyses**

First, we wanted to identify regions of the brain that increase with working memory load, regardless of whether the content dealt with in working memory is social or cognitive. To examine this, at the first level of analysis, we modeled linear changes in neural activity as a function of working memory load (i.e., parametric modulation analysis) separately for SWM and CWM tasks. At the second level of analysis, we then performed a conjunction analysis of SWM and CWM parametric modulation analyses. Results from the conjunction analysis showed that regions of the lateral frontoparietal system (bilateral dorsolateral prefrontal cortex (DLPFC), bilateral inferior parietal lobule (IPL), middle frontal gyrus (MFG), and supplementary motor area (SMA), *Supplementary Figure 1, Supplementary Table 1*), parametrically increase their activity with load, regardless of whether the working memory processes engaged are social or cognitive.

To isolate the neurocognitive mechanisms that specifically support SWM, we directly compared parametric increases as a function of load (i.e., parametric modulation analyses).
between SWM and CWM trials. This analysis identified regions that were more strongly modulated by SWM load level than CWM load level. Results revealed robust activation of the mentalizing system (dorsomedial prefrontal cortex (DMPFC), precuneus/posterior cingulate cortex (PC/PCC), right tempoparietal junction (rTPJ), as well as ventromedial prefrontal cortex (VMPFC); Figure 4, Table 1). The only other region of the brain that showed activation in this analysis was a cluster of lingual gyrus in the visual cortex. We decomposed this effect in mentalizing regions by looking at parameter estimates from the four mentalizing clusters observed in this analysis for each working memory load level separately for SWM and CWM trials. This revealed that the mentalizing regions linearly increase as a function of SWM load, but decrease as a function of CWM load (plotted parameter estimates in Figure 3 highlight the decomposition of this effect). It is worth noting that the 3 load and 4 load SWM trials all produced effects in these clusters that were higher than activation during the implicit baseline in which participants rest while looking at a fixation cross-hair.

*Predicting Perspective-Taking from Parametric Modulation in the Mentalizing System.*

Past working memory research has found that individual differences in lateral frontoparietal system activation during working memory corresponds with individual differences in other, related cognitive capacities, such as math and reading ability (Ashkenazi, Black, Abrams, Hoeft, & Menon, 2013; Dumontheil & Klingberg, 2011; Metcalfe, Ashkenazi, Rosenberg-Lee, & Menon, 2013), as well as IQ (Gray et al., 2003). By extension, to the extent that the mentalizing system functions as a SWM system, ramping up as it juggles more pieces of social information simultaneously, individual differences in its activation during SWM should also correspond with individual differences in other social cognitive capacities, such as perspective-taking.
To examine this possibility, we pulled parameter estimates from the clusters observed in the contrast comparing SWM load vs. CWM load parametric modulation effects (DMPFC, PCC, rTPJ, VMPFC). These values were then each entered as a predictor variable in separate linear regressions with third person-perspective taking accuracy, controlling for first-person perspective taking accuracy, as the dependent variable. Results showed that the DMPFC, PC/PCC, VMPFC, and marginally rTPJ parametric difference values predict individual differences in perspective-taking (Figure 5; Table 1).

Importantly, these effects mostly appear to be driven by parametric changes in mentalizing regions during SWM (results from the same clusters, but examining parameter estimates from the SWM parametric modulation effect only: DMPFC $\beta=.48$, $p=.02$; PCC $\beta=.38$, $p=.06$; VMPFC $\beta=.5$, $p=.01$; rTPJ $\beta=.28$, $p=.17$), rather than during CWM (results from the same clusters, but examining parameter estimates from the CWM parametric modulation effect only: DMPFC $\beta=-.24$, $p=.25$; PCC $\beta=-.34$, $p=.10$; VMPFC $\beta=-.25$, $p=.23$; rTPJ $\beta=-.25$, $p=.22$). Thus, general working memory load effects do not drive the relationship with perspective-taking per se, but instead the tendency to increase activity in mentalizing regions during higher levels of SWM load.

To further examine the specificity of these effects, we performed two follow-up analyses. First, we pulled parameter estimates from the left DLPFC and IPL regions observed in the conjunction analysis above. These are both canonical working memory regions and parameter estimates from the SWM trials did not predict perspective-taking performance (IDLPFC SWM $\beta=.04$, $p=.84$, IPL SWM $\beta=.10$, $p=.64$). Parametric activation in IDLPFC during CWM showed a negative relationship with perspective-taking that trended toward significance ($\beta=-.39$, $p=.06$), although IPL showed no relationship with perspective-taking ($\beta=-.14$, $p=.49$). Thus, while
parametric increases in mentalizing regions during SWM may contribute to perspective-taking ability, the tendency to parametrically increase activity in IDLPFC during CWM may potentially interfere with perspective-taking.

Second, we examined whether the effects were somehow a byproduct of general social information processing rather than tied to SWM specifically. Pulling parameter estimates from the same four mentalizing regions from a contrast of SWM, collapsing across load level, and baseline revealed no significant relationships with perspective-taking performance (DMPFC $\beta=.13$, $p=.53$; PCC $\beta=.04$, $p=.83$; rTPJ $\beta=.05$, $p=.82$ VMPFC $\beta=.02$, $p=.94$). Thus, the extent to which mentalizing regions increase their activity under SWM load, but not CWM load, is predictive of perspective-taking performance on the Director’s task.

**Discussion**

Research on social cognition has typically assumed that the cognitive demands afforded by challenging social cognitive processing engage the same psychological mechanisms as those supporting other, non-social forms of effortful cognition (e.g., (Gilbert, Pelham, & Krull, 1988)). Here, we show that while both SWM and CWM recruit the lateral frontoparietal system, the medial frontoparietal system associated with mentalizing differentially engages during SWM. Specifically, the mentalizing system linearly increased activation as a function of SWM load (i.e., the number of friends considered along a trait dimension during a delay period), but decreased as a function of CWM load (i.e., the number of friends’ names alphabetized during a delay period). What is more, linear increases in activation in mentalizing regions, but not lateral frontoparietal regions, positively predicted perspective-taking ability. Thus, the working memory demands afforded by challenging social cognitive processing may rely on domain-specific social cognitive mechanisms.
These results revise our understanding of mentalizing system function. Traditionally, medial frontoparietal regions associated with mentalizing have been considered regions that support non-effortful forms of cognitive processing (Greicius & Menon, 2004; McKiernan et al., 2003). Indeed, past working memory research using CWM paradigms find that medial frontoparietal region activity during CWM actually interferes with CWM performance (Anticevic et al., 2010). However, none of this prior work engaged working memory with mentalizing-related content. Our results suggest that these regions may have controlled-processing properties specifically for social cognitive information processing.

That said, it is interesting to consider that a large literature finds that these medial frontoparietal regions are also highly active during periods of idle rest (Gusnard, Akbudak, Shulman, & Raichle, 2001; M. Raichle & Snyder, 2007; Spreng et al., 2009). In fact, research in cognitive neuroscience tends to refer to the functional network that comprises mentalizing regions as the ‘default network,’ because the regions appear to engage when participants are resting, or ‘by default.’ Interestingly, all of the mentalizing regions active during 3-friend and 4-friend SWM trials showed activation higher than the fixation baseline (which can be considered brief periods of rest). This observation is important because prior work using easier social cognitive tasks often found increased activation in mentalizing regions relative to a control condition, but nonetheless decreased activation in mentalizing regions relative to a fixation baseline. Such findings made it difficult to rule out the possibility that medial frontoparietal regions are more sensitive to ‘easy’ cognitive processing, than social cognitive processing per se. Finding that medial frontoparietal regions are more active than fixation for more challenging SWM trials is inconsistent with this possibility, suggesting these regions are more sensitive to
the degree of social cognitive processing, rather than less challenging cognitive processing engaged during rest.

Considering the SWM findings and the default network literature side-by-side begs the question as to why the same regions that support externally-generated (e.g., stimuli-induced) social cognitive challenges also engage rather automatically when individuals are not required to attend to externally-generated, non-social stimuli. One possibility is that, given the importance of understanding the social world around us, engaging medial frontoparietal regions during rest may facilitate the ability to effortfully engage these regions during and/or consolidate information learned after externally induced social cognitive challenges. Future research linking default network activation and/or functional connectivity during rest to linear increases during SWM may shed light on these possibilities and clarify the psychological function of medial frontoparietal regions’ activity during rest.

In addition to amending our understanding of mentalizing system function, these results also update psychological theories of effortful social cognition. That is, it has been assumed that in processes ranging from attribution to self-regulation, poor social cognitive performance caused by cognitive load reflects the taxing of a single pool of cognitive resources. For example, if participants are required to simultaneously engage CWM when encoding a person’s behavior, they are more likely to commit the ‘fundamental attribution error,’ or demonstrate a bias to assume that brief behavioral displays (e.g., a woman nervously waiting for a job interview) are guided by enduring personality traits (e.g., she is a very nervous person in general), rather than the social context (e.g., waiting for a job interview may make anyone appear nervous and thus the woman’s behavior is not prescriptive of her personality in general; Gilbert et al., 1988). Findings such as these have led to the interpretation that cognitive and social cognitive demands
share a limited pool of resources, and thus taxing this pool with cognitive load renders these resources unavailable for social cognitive processing. However, if this were the case, then SWM load would only linearly increase lateral frontoparietal regions associated with CWM, and no other neural activation would be distinct. Instead, while SWM and CWM load both linearly increased activation in lateral frontoparietal regions, SWM load linearly increased activity in mentalizing regions, whereas CWM load decreased these same mentalizing regions. Thus, poor social cognitive performance caused by cognitive load may partially reflect the shared recruitment of the lateral frontoparietal system, but also perhaps, the inhibition of the mentalizing system needed to handle effortful social cognitive demands. Moving forward, social psychologists interested in whether their construct of interest exhausts cognitive resources may gain more traction by asking whether their construct exhausts cognitive resources, social cognitive resources, or both.

It is noteworthy that while linear increases in mentalizing regions as a function of SWM load positively predicted perspective-taking performance, linear increases in DLPFC, a region consistently associated with CWM (Curtis & D'Esposito, 2003), as a function of CWM load negatively predicted perspective-taking ability. On the one hand, this pattern may suggest that while SWM properties in mentalizing regions contribute to social cognitive ability, CWM properties in DLPFC may actually interfere with social cognitive ability. This possibility is on par with past research finding that regions associated with mentalizing and the lateral frontoparietal systems tend to compete with one another (Greicius & Menon, 2004; McKiernan et al., 2003; Metzak et al., 2011). On the other hand, it is possible that different kinds of working memory properties in these regions relate to social cognitive ability. That is, while efficient processing, indexed by less activation in response to CWM load, in canonical working memory
regions may contribute to better social cognitive ability, intentional recruitment, as indexed by *more* activation in response to SWM load, in mentalizing regions may contribute to better social cognitive ability. Future research that pits these different interpretations against one another may help clarify why medial and lateral brain regions’ activation during these forms of working memory may differentially relate to social cognitive skills.

Finally, these results have interesting implications for understanding social cognitive deficits in clinical disorders. For certain clinical disorders, such as schizophrenia, social cognitive deficits persist in tandem with non-social cognitive deficits (Couture et al., 2006; Goldman-Rakic, 1994; Pickup & Frith, 2001). In other disorders, such as autism spectrum disorder (ASD), social cognitive deficits persist (Baron-Cohen et al., 1985; Dawson & Fernald, 1987) even though non-social cognitive ability can be spared (Bennetto et al., 1996; Ozonoff & Strayer, 2001). Importantly, most prior social cognitive tasks assessing brain function that tend to be used in studying these populations’ social cognition are very easy, in terms of mental effort (e.g., the false-belief task used to assess ‘theory of mind’ is passed by most typically developing five-year olds (Sommer et al., 2007; Wimmer & Perner, 1983). Incorporating SWM paradigms, as well as examining the link between SWM ability and perspective-taking, in the study of these clinical populations may therefore be useful in clarifying in these populations 1) how the mentalizing system and lateral frontoparietal system may function and interact in response to more challenging forms of social cognition and 2) the extent to which the ability to linearly recruit these systems during SWM relate to everyday social skills.

**Conclusion**

In conclusion, these findings suggest that contrary to prior assumptions, working memory for social cognitive information is not simply another case of generic working memory
mechanisms applied to social information. SWM differentially recruited the neural system associated with mentalizing, and the ability to engage the mentalizing system, but not lateral frontoparietal system associated with generic forms of working memory, predicted performance on an objective measure of perspective-taking ability. Together, these findings suggest that social working memory is a construct worthy of scientific study that ultimately may help us better understand how humans decipher and make meaning of the social world around them.
Figure 1. Pictorial display of the (A) social working memory (SWM) task and (B) cognitive working memory (CWM) task. Each trial included encoding (4 secs), instruction (1.5 secs), delay (6 secs), and the true/false probe question (4 secs).
Figure 2. Pictorial display of the Director’s Task. For each trial, the participant viewed the first slide and heard the Director ask for one of the objects on the shelf to be moved (2.5 seconds). One the next screen, the participant saw an arrow indicating one of the objects to be moved and determined whether the arrow indicated the object that the director asked to be moved (up to 5 secs).
Figure 3. Average reaction times for each working memory load level, separately plotted for social working memory (SWM) and cognitive working memory (CWM) tasks.
Figure 4. Whole-brain results from the comparison of social working memory (SWM) load effects versus cognitive working memory (CWM) load effects (i.e., differences in linear increases as a function of load for SWM compared to CWM).
Figure 5. Scatter plots of linear regression results predicting perspective-taking performance from linear increases in mentalizing regions as a function of social working memory (SWM) vs. cognitive working memory (CWM) load. X-axes are mentalizing cluster parameter estimates and Y-axes are perspective-taking performance.
Supplementary Figure 1. Whole-brain results from the conjunction of social working memory (SWM) and cognitive working memory (CWM) load effects. Green indicates regions associated with SWM load effects, blue indicates regions associated with CWM load effects, and pink indicates regions associated with load effects for both SWM and CWM. There were no unique clusters of activation in medial slices of the brain and therefore medial views are not displayed.
Table 1. Brain regions showing differential parametric increases as a function of Social Working Memory (SWM) load versus Cognitive Working Memory (CWM) load.

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Table 2. Results from linear regressions with each mentalizing region from SWM load modulation effect (vs. CWM load effect) as an independent predictor of perspective-taking ability.

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Supplementary Table 1. Clusters showing significant activation in the conjunction of working memory load across Social Working Memory (SWM) and Cognitive Working Memory (CWM) tasks.

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References


PAPER 3:

Is social cognition plastic? Social working memory training improves social cognitive ability
Abstract

Social cognitive ability is imperative for everyday success in a social world. And yet, even healthy adults often fail to accurately understand the thoughts, feelings, and intentions of those around them. The present study examined, for the first time, whether social cognitive ability in adults is plastic and can be improved with training. Building on recent findings from the cognitive working memory (CWM) training literature, we employed a novel social working memory (SWM) training intervention to test whether SWM can be improved with training and whether SWM training corresponds with improved social cognitive reasoning (perspective-taking performance). Participants were randomly assigned to complete SWM training or CWM training (an active control condition) and pre-training versus post-training changes in SWM, CWM, and perspective-taking performance were assessed. Both training interventions improved these three outcome measures. However, individuals with more autistic traits yielded the greatest gain in SWM after undergoing SWM training, but not CWM training. Thus, those who have the most to gain in the ability to manage social information in mind may reap the most improvement from SWM training, rather than CWM training. Moreover, social cognitive gains in perspective-taking performance from pre-to-post training were positively correlated with SWM training improvements, but not CWM training improvements. Together, these results suggest that social cognitive ability in adults is plastic and can be improved, potentially, by different routes via SWM and CWM training.

Without an ability to understand those around us, humans would not get very far. Everyday success requires the ability to understand and connect with others, and social competence has been linked to a variety of positive outcomes such as health (Cohen, Sherrod, & Clark, 1986), relationship satisfaction (Franzoi, Davis, & Young, 1985), and even leadership (Zaccaro, Gilbert, Thor, & Mumford, 1991). Yet, while social competence is critical to everyday life, people frequently fall short in their ability to discern what other people think and feel. For example, healthy adults frequently misinterpret what another person is thinking (Apperly, Back, Samson, & France, 2008; Apperly, Riggs, Simpson, Chiavarino, & Samson, 2006; Keysar, Barr, Balin, & Brauner, 2000), are biased in their attributions of other’s behaviors (Jones & Nisbett, 1971), and are often inaccurate in inferring another person’s emotional state during communication (Zaki, Weber, Bolger, & Ochsner, 2009).

That even healthy adults’ social cognitive ability is imperfect begs the question of whether and how social cognitive ability can be improved. While a few studies have shown that practicing social cognitive exercises (e.g., imagining different character’s perspectives in a story improves social cognitive performance in clinical and developing samples (Chalmers & Townsend, 2014; Combs et al., 2007; Fisher & Happé, 2005), virtually no research systematically examines the mechanisms through which social cognition may be improved, nor whether social cognitive ability is plastic among healthy adults.

One possible mechanism facilitating plasticity in social cognition may be working memory training. Working memory, or the ability to maintain and manipulate information in mind, is associated with a variety of cognitive skills and recent research suggests that working memory training may not only improve working memory capacity (e.g., the amount of
information that can be managed in mind at once), but may also improve performance on related
cognitive tasks, such as those assessing reading and math ability (Chein & Morrison, 2010;
Holmes, Gathercole, & Dunning, 2009), inhibition (Klingberg et al., 2005), and even fluid
intelligence (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; Jaeggi, Buschkuehl, Shah, & Jonides,
2014). For example, healthy adults randomly assigned to complete working memory training for
8-19 days showed improvements in working memory capacity and gains in fluid intelligence
post-training, with those individuals undergoing the most days of training yielding the greatest
gains (Jaeggi et al., 2008). Thus, working memory training may be a potential route to improved
cognitive ability, even among healthy adults.

Of interest to the possibility that working memory training may improve social cognitive
skills is the observation that brain regions associated with social cognitive reasoning appear to
have working memory properties. That is, we recently showed that a medial frontoparietal
neurocognitive system associated with thinking about peoples’ mental states and personalities, or
‘mentalingiz,’ shows linear increases in activation as a function of the number of people’s traits
considered during working memory (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012;
Meyer, Taylor & Lieberman, in prep), a response pattern characteristic of working memory
systems (Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999). Moreover, linearly
increasing activation in medial frontoparietal brain regions associated with mentalizing predicted
individual differences in trait and laboratory measures of perspective-taking ability (Meyer et al.,
2012, Meyer, Taylor & Lieberman, in prep). Thus, given that brain regions associated with
mentalingiz may have working memory properties that link to measures of social cognitive
ability, like perspective-taking, training social working memory (SWM) may likewise lead to
improvements in SWM performance, as well as yield transfer effects to perspective-taking.
To examine these possibilities, participants were randomly assigned to complete twelve days of either SWM training or cognitive working memory (CWM) training (an active control condition). The rationale of using CWM training as an active control condition was that past research has already shown the CWM training can improve performance on both working memory tasks and other tasks that also require managing information in mind, but that are not working memory tasks trained. Thus, CWM training should improve SWM performance and performance on a perspective-task that requires subjects to mentally refer to another person’s state of mind. Showing that SWM training not only also improves these outcomes, but also may uniquely improve these outcomes, relative to CWM training, would thus be the strictest test of whether SWM training may improve these outcomes through at least partially unique SWM mechanisms. One day prior to training, participants completed baseline measures of SWM and CWM performance, as well as perspective-taking ability (measured by a variant of the Director’s Task (Dumontheil, Küster, Apperly, & Blakemore, 2010; Keysar et al., 2000)). One day after training, participants completed unique trials of the same pre-training tasks. It was predicted that SWM and CWM training would not only correspond with improved SWM task performance post- vs. pre-training, but also improved perspective-taking performance post- vs. pre-training, which would suggest that the benefits of SWM/CWM training may transfer to other, related social cognitive abilities. Moreover, given our previous observations that brain regions associated with social cognition have working memory properties specific to SWM, and that recruiting these brain regions during SWM uniquely relates to perspective-taking ability, we explored the extent to which SWM (vs CWM) training may uniquely improve perspective-taking performance.

**Methods**
Participants

68 participants were recruited (36 female, Mean age=21.14, SD=2.69) from the University of California, Los Angeles (UCLA) community to participate in the study. Eleven recruited participants did not complete their working memory training and therefore were paid for the aspects of the study they completed, did not undergo post-training laboratory sessions, and were excluded from analyses, yielding a total of 57 subjects (30 in the SWM training condition (14 males, 16 females, Mean Age=21.45, SD=3.43) and 27 in the CWM training condition (13 males, 14 females, Mean Age=20.9, SD=2.04). Participants were paid $180 and provided written informed consent according to the procedures of the UCLA Institutional Review Board.

Procedure

Pre-training and Post-training Laboratory Sessions

As in Studies 1 and 2, two weeks prior to participation, participants completed the friend trait-rating questionnaire for ten of their close friends (Figure 1). For each trait, participants rated how much each of the friends possesses the trait on a 1-100 scale (1 being the least and 100 being the most). These ratings were later used to create SWM trials (see Materials). Participants completed two laboratory sessions. In Laboratory Session 1, participants completed the computerized SWM/CWM task used in Study 2 to measure baseline SWM and CWM performance. This task comprised 18 SWM trials (6 with 2 friends encoded, 6 with 3 friends encoded, and 6 with 4 friends encoded) and 18 CWM trials (6 with 2 friends encoded, 6 with 3 friends encoded, and 6 with 4 friends encoded). The 18 trials of each working memory type were pseudorandomized and presented in blocks of 9 trials, with the cue ‘traits’ or ‘alphabetize’
shown prior to each block, so that subjects knew which trial type they were going to complete next.

Participants also completed the Director’s Task (Figure 2), a computerized measure of perspective-taking ability, which comprised 18 trials. In this task, participants observe a set of objects on a bookshelf. A woman by the bookshelf (the ‘Director’) first asks (via audio-recording) the participant to move one of the objects that appears on the shelf (2.5 seconds). Participants next have up to 5 seconds to determine whether an arrow suggesting one of the objects to be moved is the object that the director wanted to be moved. Some of the shelves on the bookshelf have a wall behind them and others do not. For first-person perspective trials (6 trials), the director faces the front of the bookshelf (and therefore has the same perspective as the participant) and asks for one of three objects within a category of objects to be moved (e.g., “move the top tickets down”). For third-person perspective trials (6 trials), the director is on the other side of the bookshelf and therefore has a different perspective than the participant. This director also asks for one of three objects within one category of objects to be moved (e.g., “move the top tickets down”). For both of these first-person and third-person perspective trials, at least one of the objects relevant to the director’s request is on a bookshelf blocked by a wall. As a result, only third-person perspective trials require the participant to make a decision based on whether or not the director can see the object. Third-person perspective-taking trials therefore isolate perspective-taking ability, whereas first-person perspective taking trials are cognitively matched except for the fact that they do not require representing the director’s perspective to determine a correct answer. Six trials (3 first-person perspective trials and 3 third-person perspective trials) were catch trials in which a director asked one object in one category of objects to be moved (e.g., “move the popcorn down”). The order of presentation of the total set
of 18 Director Task trials was randomized. On the fourteenth day after the participant’s first laboratory session, participants completed their post-training laboratory session. In this post-training laboratory session, participants also completed the SWM/CWM task and the Director’s task. The number of trials per condition for each of these runs was identical to the pre-training session. However, all trials presented in the post-training session were unique from those presented in the pre-training session. In both laboratory sessions, participants completed practice trials of each task immediately before completing a given task. Participants completed 3 SWM trials and 3 CWM trials before they completed the working memory tasks, and 4 Director Task trials before completing the Director’s Task.

Training Paradigm

Participants were randomly assigned to complete SWM or CWM training. Training comprised 12 days of working memory exercises. Each daily set of working memory exercises included 60 trials of training, which collectively yielded a total ~20mins/day of training. Consistent with past working memory training research (e.g., Holmes et al., 2009; Jaeggi et al., 2008; Klingberg et al., 2005), working memory training was computer-adaptive based on the subject’s performance. For each set of five trials, participants answered working memory trials of the same load level (e.g., 2 friends, 3 friends, 4 friends, etc, with a maximum of 6 friends). If the participant answered more than three of the five working memory trials correctly, the following five trials presented were of a greater load level (e.g., if a participant answered four or more three-load trials correctly, the next set of five trials showed four friends). If the participant answered less than three trials correctly, the following set of five trials showed a lower load level (e.g., if participants answered two or less three-load trials correctly, the next set of five trials showed two friends). If the participant answered three trials correctly, the following set of five
trials showed the same load level as the previous five trials. SWM training trials were determined accurate if the participants’ answer was consistent with their original online trait rankings, a method previously shown to be successful in determining SWM accuracy (Meyer et al., 2012).

Participants completed working memory training sessions online by logging into a website with their subject ID number. On the first day of training, the first five working memory trials began with the easiest (two friend) load level. Each subsequent training session began with five trials of the load level of the previous day’s maximum load level. That is, if on the first day of training, the subject’s maximum number of friends considered was five, the first five trials on the second day of training showed five friends. To facilitate participant compliance, participants received two emails/day (once in the morning and once in the evening) to remind them to complete their online exercises.

**Materials**

For each SWM trial, participants encoded the names of 2, 3, or 4 friends selected from a list of their 10 close friends that they provided 2 weeks before the scan. Consistent with the original SWM study (Meyer et al., 2012), to control for rating distance effects on task difficulty, we aimed to select friends that were ranked no more than 25 points apart (on the 100-point scale) and no closer than 5 points apart from one another for each trait word. These distances served as a rule for friend name selection for both the laboratory sessions and training sessions and were adhered to as closely as possible given the distribution of ratings given by the participants (Mean distance for friend names within a trial=13.26; SD=4.27). Each participant was shown their own friends’ names on each trial. For both the SWM task and the Director’s task, trials were standardized on brightness, contrast, font, and size.

Two weeks prior to the first laboratory session, participants completed the Autism
Quotient (AQ), a measure of autistic traits (S Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). A hallmark trait of Autism Spectrum Disorder (ASD) is poor social cognitive competence, and thus AQ scores served as an index of social cognitive ability within a healthy (non-clinical) population. AQ scores are computed by summing the number of endorsed autistic tendencies. For example, endorsing statements such as, “I find it difficult to work out people's intentions,” would count as one point towards an AQ score, whereas endorsing statements such as “I find social situations easy” would not. The maximum AQ score is 50, with individuals diagnosed with ASD scoring 32 points or higher (Baron-Cohen et al., 2001).

Data analysis

All analyses compared performance on tasks pre- versus post-training. To examine how gains in SWM and CWM training relate to gains in Director’s Task performance, we computed the following variables. First, for each subject we computed a value measuring the extent to which their difference in reaction time (RT) between easy (2 friend) and hard (4 friend) trials was reduced after training, separately for SWM and CWM task performance, which would indicate greater efficiency post-training, and is therefore referred to as ‘efficiency gain.’ In other words, to the extent that RT on hard (4 friend) trials becomes more similar to RT on easy (2 friend) trials, the greater gain in efficiency for hard working memory trials. To do this, the following variables were computed: SWM ‘efficiency gain’=(SWM RT 4 Friend Trialspre-training – SWM 2 friend trialspre-training)-(SWM RT 4 Friend Trialspost-training – SWM 2 friend trialspost-training) and CWM ‘efficiency gain’=(CWM RT 4 Friend Trialspre-training – CWM 2 friend trialspre-training)-(CWM RT 4 Friend Trialspost-training – CWM 2 friend trialspost-training). Second, to relate actual training performance to transfer effects on the Director’s Task, we computed the overall accuracy across training trials. Because SWM and CWM training
interventions were computer-adaptive based on performance, this variable should reflect gained improvement (i.e., the more correctly answered trials, the greater increases in task difficulty) in SWM or CWM, respectively for each training condition.

To examine how these working memory gain variables link to improvements in perspective-taking, we computed the following variable to isolate specifically the perspective-taking portion of the Director’s Task. Consistent with the perspective-taking score developed in Study 2, we computed gains in third-person perspective-taking trial accuracy, controlling for gains in first-person perspective-taking accuracy (i.e., the unstandardized residuals resulting from the regression of first-person perspective accuracy gain on third-person perspective accuracy gain). This variable isolates perspective-taking gain, independent of the gains to the non-social processes engaged in the Director’s Task, and is referred to as ‘Direct Task perspective-taking gain.’

To ensure outliers did not affect results, data points > 2.5 SDs below or above the mean were winsorized by moving the data point to 2.5 SDs from the group mean. Seven values across all examined variables were winsorized. In the SWM training group, one AQ score, one value of efficiency gain in SWM RT, and one value of Director’s Task perspective-taking gain were winsorized. In the CWM training group, two values of Director’s Task perspective-taking gain, and two values of percent of correctly answered trials throughout training were winsorized.

Results

*Autism Quotient (AQ).*

The mean AQ score for the entire sample was 17.59, SD=4.81, with the mean AQ score
for the SWM training group=17.38, SD=4.69 and the mean AQ score for the CWM training group=18, SD=4.94. Mean AQ scores did not significantly differ across training groups (p=.54), and the sample means are consistent with those previously reported in healthy samples not diagnosed with ASD (Baron-Cohen et al., 2001).

Training Manipulation Checks.

Because this is the first study to employ a SWM training paradigm, we examined the following statistics to ensure computer-adaptive SWM training works. In the SWM training condition, the average load level attained across training was 4 friends (SD=.87) and the final peak load level achieved was 3.93 (SD=1.46), suggesting SWM computer-adaptive training works (e.g., participants’ performance can adapt, since all participants began training with 2 friend trials). Although compared to SWM training, CWM training was associated with significantly higher average load level achieved (mean=5.66, SD=.77, t(55)=7.59, p<.0001), and higher final peak load level achieved (mean=5.79, SD=.75, t(55)=5.94, p<.0001), average RT across the two groups’ training trials were not statistically different from one another (average RT in the SWM training group =1.64 secs (SD=.31 secs) and average RT for the CWM training group=1.75 (SD=.22); (t(55)=1.42, p=.16).

SWM can be improved with training.

The primary goal of this study was to examine whether SWM, like CWM, can be trained. We replicated past CWM training studies, finding that CWM training corresponded with improved CWM performance, as well as SWM performance (faster RT post vs. pre training (Figure 3). In addition, and for the first time in the working memory and social cognition literatures, we observed that SWM training improved SWM and CWM performance (faster RT
post vs. pre training (Figure 3)). More specifically, RT for each load level showed significant gains in speed post vs. pre training for both the SWM and CWM training groups. There was no significant difference in the amount of RT gain between training groups, for any of the load levels across the SWM or CWM trials (ps>.21). Among individuals who underwent SWM training, however, there was a significant relationship between AQ score, an index of autistic traits, and gains in SWM speed for the most challenging (4 friend) trials (r=.36, p=.05, Figure 4) as well as a trend towards significance for the relationship between AQ scores and gain in CWM speed for the most challenging (4 friend) trials (r=.30, p=.12). In contrast, among individuals who underwent CWM training, AQ scores did not significantly correlate with improvement in either forms of working memory (ps>.30). Thus, although both forms of WM training correspond with improvements in SWM and CWM performance, SWM training may be most beneficial for those individuals with the greatest need to improve their ability to manage social information in mind.

Transfer effects of SWM and CWM training

The second goal of the present study was to examine if, just as CWM training has been shown to improve performance on related cognitive tasks (Chein & Morrison, 2010; Holmes et al., 2009), SWM training leads to improved social cognitive performance on a related social cognitive task, here perspective-taking performance on the Director’s Task. We found that both SWM and CWM training corresponded with improved performance on the Director’s Task (Figures 5, 6). In both training groups, participants’ RT gained significant speed on first-person perspective and third-person perspective trials as well as accuracy on third-person perspective trials (Table 1). Moreover, while participants’ accuracy on first-person perspective trials was almost at ceiling pre-training, (92% correct for the SWM training group, SD=12%; 94% correct
for the CWM training group, SD=10%), there were trends towards significant improvement post-training (96% correct for the SWM training group, SD=10% (t(29)=1.53 p=.14; 98% correct for the CWM training group, SD=5% (t(26)=1.65, p=.11). Interestingly, while accuracy was significantly worse on third-person perspective trials than first-person perspective trials pre-training in both training groups (ps<.0001), this relationship became non-significant for individuals who underwent SWM training (p=.26), but stayed marginally significant for individuals undergoing CWM training (t(26)=1.76, p=.09).

**Do SWM and CWM training improve perspective-taking through different mechanisms?**

We next performed a set of correlations to more closely examine the possibility that SWM training may lead to improvements in the Director’s Task through, at least partially, different mechanisms than CWM training. To examine this possibility, we first correlated Director’s Task perspective-taking gain with 1) SWM efficiency gain in the SWM training sample and 2) CWM efficiency gain in the CWM training sample with the rationale that each training condition is most directly improving the form of WM trained. None of these gain variables differed significantly between the two training groups (ps>.81), and therefore group mean differences do not drive the reported correlation results. Among individuals who underwent SWM training, SWM efficiency gain showed a significant positive correlation with Director Task perspective-taking gain (r=.41, p<.05, Figure 7). In contrast, among individuals who underwent CWM training, Director Task perspective-taking gain did not correlate with CWM efficiency gain (r= -.04, p=.85) and this correlation was marginally statistically different from the one found in the SWM sample (Fisher’s z=1.7, p=.08).

Consistent with the findings that SWM efficiency gain pre-to-post training correlate with perspective-taking improvement, performance on the actual SWM training intervention also
appears to relate to Director Task perspective-taking gain. In the SWM training group, the percentage of correctly answered SWM trials throughout training correlated with Director Task perspective-taking gain \((r=.36, p=.05, \text{ Figure 8})\). However again, in the CWM training group, the percentage of correctly answered CWM trials throughout training did not correlate with Director Task perspective-taking gain \((r= -.24, p=.17)\), and this correlation was statistically different from the one observed in the SWM training group \((\text{Fisher’s } z=2.22, p<.05)\). Thus, SWM training may improve perspective-taking directly through SWM mechanisms, whereas CWM training may improve perspective-taking performance through other mechanisms that do not directly relate to the ability to represent another person’s point of view.

**Discussion**

Research in social cognition consistently finds that even healthy adults are often inaccurate in their ability to understand other peoples’ mental states, traits, and perspectives (Apperly et al., 2008; Keysar et al., 2000). Despite the many known errors in adult social cognition, to date virtually no work has examined whether adult social cognitive ability may be plastic, and improved with training. Here, we found that working memory training improves social cognitive performance on a classic measure of perspective-taking that is known to be challenging for even healthy adults: the Director’s Task (Keysar et al., 2000). Moreover, SWM training (but not CWM training) specifically related to improvement in perspective-taking, independent of improvements in non-social processing engaged in the Director’s Task.

These results compliment and extend a growing area of research on the benefits of cognitive training, as they are the first to examine the effects of working memory training on social cognition. Past working memory training research has found the CWM training improves CWM capacity and leads to improvements on other, related cognitive tasks (Chein et al., 2010;
Holmes et al., 2009; Jaeggi et al., 2008; 2014). By extension, we found that both SWM and CWM training improve SWM capacity (e.g., greater speed post-vs-pre training), as well as perspective-taking performance. Consistent with past research showing that different working memory strategies can be trained, and that these strategies can relate to transfer effects in different ways (Turley-Ames, 2003), only SWM training appears to directly relate to perspective-taking gains on the Director’s Task. That is, among individuals who underwent SWM training, SWM efficiency gain correlated positively with Director Task perspective-taking gain, whereas in individuals who underwent CWM training, CWM efficiency gain showed no relationship with Director Task perspective-taking gain. Thus, SWM and CWM training may improve perspective-taking via different information processing mechanisms, with SWM training directly improving mental state representation.

The possibility that the two training interventions may improve perspective-taking via different information-processing mechanisms has interesting implications for training social cognition in clinical populations. Several clinical populations that suffer from social cognitive deficits show either dual or differential deficits in CWM. For example, research on autism spectrum disorder (ASD) finds that social cognition is impaired (e.g., Baron-Cohen et al., 2003) even though CWM ability is often intact (Ozonoff & Strayer, 2001). Interestingly, in our non-clinical sample, individuals who endorsed more autistic traits as indexed by the Autism Quotient (AQ), showed significant improvement in performance on challenging (4 friend) SWM trials if they underwent SWM training, but not CWM training. Given that problems in managing social information in mind associated with ASD may be specific impairments in social cognition (Simon Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003), these results suggest that individuals with ASD may reap the most benefits in social cognition from SWM
training interventions, rather than CWM training interventions. In contrast, individuals with schizophrenia show dual deficits in social cognition and working memory (Couture, Penn, & Roberts, 2006; Lee & Park, 2005), and their working memory deficits correlate with their deficits in social cognition (Vauth, Rüsch, Wirtz, & Corrigan, 2004). Thus, individuals with schizophrenia may benefit most from working memory interventions that combine SWM and CWM training.

The possibility that SWM and CWM training interventions may improve social cognition via different mechanisms is consistent with the neuroimaging findings reported in Study 1 and Study 2. Studies 1 and 2 find that SWM relies on two large-scale neurocognitive networks: the lateral frontoparietal system associated with CWM and the medial frontoparietal system associated with mentalizing, or the ‘mentalizing system.’ In fact, the mentalizing system shows a full dissociation across SWM and CWM: this system increases as a function of SWM demands, but decreases as a function of CWM demands. Thus, SWM training may lead to changes in either the lateral frontoparietal network, mentalizing network, or both. In contrast, CWM training may lead to changes in the lateral frontoparietal network, and perhaps, actually lead to an increased suspension of the mentalizing network. That is, because the mentalizing system decreases as a function of CWM load (a pattern found in Study 2 as well as past cognitive neuroscience research (McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003), and CWM load increases as a function of improved performance on CWM training trials, CWM training may actually lead individuals to suppress the mentalizing system. Future research examining neural changes in the lateral frontoparietal and mentalizing networks from pre-to-post training should help clarify the exact mechanisms through which SWM and CWM training lead to
changes in SWM and CWM capacity, as well as transfer effects on social cognitive tasks such as perspective-taking.

Limitations

This is the first study to examine SWM training and its potential transfer effects and thus it is not without unforeseen limitations. First, since the publication of the CWM training studies that inspired the present study, there have been a number of research findings and reviews that question the extent to which transfer effects from working memory training are real and long-lasting (Conway & Getz, 2010; Melby-Lervåg & Hulme, 2013). The present findings potentially suffer from some of the same criticisms. For example, from the present study, it is unclear how long improvements on the director’s task last, as well as whether they correspond with improved perspective-taking in participants’ everyday life. Second, we designed the SWM and CWM training paradigms to be computer-adaptive but with a maximum number of 6 friends considered in SWM or CWM because in our prior work, accuracy on even 4-friend trials is less than 60% (Meyer et al., 2012). We therefore did not expect all participants to be able to even reach 6-friend trials. However, all subjects were able to reach this maximum load level at some point in training, and in fact most participants in the CWM training intervention remained around this peak. Future studies should remove this constriction to see how far participants’ SWM and CWM capacity can be improved, and whether individual differences in this capacity uniquely predict social cognitive outcomes. Third, although AQ correlated with gains in SWM after SWM training, AQ did not correlate with improvement on the Director’s Task, limiting the possibility that gains in SWM after SWM training transfer to social cognitive ability among those who need the most improvement. However, the AQ range in our sample was below that observed among individuals typically diagnosed with ASD (Baron-Cohen, 2001). Thus, it
remains an open question as to whether transfer effects of SWM training would be observed in samples with clinically diagnosed ASD. Fourth, because we did not have a third sample of participants who underwent no training, but who still completed the pre-post measures, it is not possible to rule out the possibility that improvements from pre-to-post training simply reflect experience with the laboratory tasks, rather than improvements from working memory training. However, it is worth noting that participants did complete practice trials of each task in each laboratory sessions, and so, in both sessions they did have practice with the task an equivalent amount in advance to completing the test trials. This provides some evidence against the possibility that improvement on the task reflects practice effects, since participants did practice prior to their first, baseline measures of each task.

Conclusion

The ability to understand people’s mental states, traits, and intentions is imperative for successful social interaction. Indeed, the ability accurately infer what another person is thinking is associated with various positive social outcomes, such as reduced stereotyping (Galinsky & Moskowitz, 2000) and greater empathy (Batson, Early, & Salvarani, 1997). Despite the pro-social side effects of understanding others’ minds, even healthy adults often inaccurately infer the minds around them (Apperly et al., 2008; Keysar et al., 2000). Here, we found that SWM training specifically improves adult perspective-taking, suggesting that adult social cognitive ability is plastic and can be improved by SWM mechanisms.
Figure 1. Pictorial display of the (A) social working memory (SWM) task and (B) cognitive working memory (CWM) task. Each trial included encoding (4 secs), instruction (1.5 secs), delay (6 secs), and the true/false probe question (4 secs).
Figure 2. Pictorial display of the Director’s Task. For each trial, the participant viewed the first slide and heard the Director ask for one of the objects on the shelf to be moved (2.5 seconds). One the next screen, the participant saw an arrow indicating one of the objects to be moved and determined whether the arrow indicated the object that the director asked to be moved (up to 5 secs).

A. “Move the top camera down.”

B. “Move the top wine bottle to the side.”
Figure 3. A. Gains in speed (reaction time (RT) in seconds) on social working memory (SWM) trials for each working memory training group and B. Gains in speed (reaction time (RT) in seconds) on cognitive working memory (CWM) trials for each working memory training group.

A. Improvements on SWM Task

B. Improvements on CWM Task

*p < .05, **p < .005, ***p < .0001,
Figure 4. Individuals with more autistic traits show the greatest improvement in hard (4 friend) social working memory (SWM) trials.

* $p<.05$
Figure 5. Gains in speed (reaction time (RT) in seconds) on Director’s Task first-person and third-person perspective trials for SWM and CWM training groups

**p<.005, ***p<.0001,
Figure 6. Accuracy Improvements on Director’s Task third-person perspective trials for SWM and CWM training groups.

***p<.0001
Figure 7. A. After undergoing SWM training, gains in SWM task efficiency positively correlate with gains in Director’s Task perspective-taking gain. B. after undergoing CWM training, gains in CWM task efficiency do not correlate with Director’s Task cognitive gains.
Figure 8. The percentage of correctly answered trials throughout SWM training positively correlate with Director’s Task perspective-taking gains.
Table 1. Changes in Director’s Task performance for social working memory (SWM) and cognitive working memory (CWM) training groups.

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<th>Pre</th>
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<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
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<tr>
<td>Reaction Time (secs) First-Person Perspective</td>
<td>1.18</td>
<td>.40</td>
<td>0.79</td>
<td>0.28</td>
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<tr>
<td>Reaction Time (secs) Third-Person Perspective</td>
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<td>0.48</td>
<td>1.03</td>
<td>0.37</td>
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<tr>
<td>Accuracy (% correct) Third-Person Perspective</td>
<td>61</td>
<td>11</td>
<td>91</td>
<td>20</td>
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References


*Proceedings of the National Academy of Sciences of the United States of America, 106*(27), 11382–7. doi:10.1073/pnas.0902666106
CONCLUSIONS

Everyday social cognition requires the ability to manage variable amounts of information about people’s beliefs, traits, and intentions. And yet, prior to this dissertation, no research had examined the basic mechanisms that allow humans to manage variable amounts of mental state information in mind. In the present dissertation, I have proposed that the online maintenance and manipulation of mental state information in mind can be characterized by what I term ‘social working memory.’ Specifically, building on past models of working memory in cognitive psychology, social working memory refers to the conscious representation, temporary storage, and/or manipulation of mental state information in mind. The findings from these dissertation studies serve as a proof of concept for the construct of social working memory. That is, participants’ show load dependent responses in reaction time, accuracy, and neural responses as a function of the number of friends’ minds managed in mind and these load dependent responses can weakened with training, all of which is consistent with theories suggesting that working memory processes are limited capacity systems (Miyake & Shah, 1999). However, and very importantly, the neurocognitive mechanisms supporting social working memory are not wholly analogous to those supporting non-social forms of working memory. That is, the medial frontoparietal network, or the ‘mentalizing system’, differentially supports social working memory processes. The results from Studies 1-3 are reviewed below and implications and future directions for this line of research on social working memory is discussed.

Study 1 found that SWM engages two neurocognitive systems: a lateral frontoparietal system associated with non-social, cognitive working memory (CWM) and a medial frontoparietal system associated with thinking about mental states, or mentalizing (the ‘mentalizing system’). Study 2 showed that working memory properties in the mentalizing
system are specific to SWM and may actually interfere with CWM. That is, the mentalizing system linearly increased as a function of SWM load (the number of friends considered along a trait dimension), but linearly decreased on a difficulty-matched CWM task as a function of CWM load (the number of friends’ names alphabetized along a trait dimension). Moreover, in Study 1 self-reported perspective-taking ability, and in Study 2 experimentally measured perspective-taking ability, correlated with linear increases in the mentalizing system, but not lateral frontoparietal system, as a function of SWM load. Thus, the working memory demands afforded by representing other people’s perspectives in mind may be supported by domain-specific working memory properties in the mentalizing system.

Finally, findings from Study 3 complement and extend the results from Studies 1 and 2 by implementing a ‘neurally inspired’ working memory training intervention. Fifty-seven participants were randomly assigned to complete a novel, computer-adaptive SWM or CWM (active-control condition) training intervention on an Internet website. Both working memory interventions improved SWM capacity and performance on the measure of perspective-taking used in Study 2. However, improvements on the perspective-taking task attributable to mentalizing only correlated with SWM training-gains in participants who underwent SWM training. In contrast, improvements on the perspective-taking task unrelated to mentalizing correlated with SWM training-gains in participants who underwent CWM training. Thus, SWM and CWM training may improve challenging forms of social cognition via different mechanisms, with SWM training perhaps uniquely improving social cognition via the mentalizing system. Future brain imaging research examining which neural mechanisms change as a function of SWM and CWM training will help determine this possibility.

Together, results from Papers 1-3 make at least three critical contributions to psychology.
First, they suggest that SWM and CWM may be very different from one another in important ways. Models of working memory have assumed that the same mechanisms supporting non-social CWM would also support working memory for mental state information. However, if linear increases in a neural region with working memory load indicates that the neural region supports working memory processes (Rypma et al., 1999), then differential linear increases in the mentalizing system as a function of SWM load suggests that SWM relies on at least partially distinct mechanisms than CWM.

Second, the neuroimaging results call into question previous assumptions about the neurocognitive networks supporting challenging, or effortful cognition. Because the mentalizing system decreases during CWM load, it has been assumed that this system interferes with effortful cognitive processing. Yet, the observation that the mentalizing system increases with SWM load suggests that this system can support social effortful processing. This observation raises several new questions and predictions about how social and cognitive load may exhaust mental resources. For example, research on stereotype threat (the phenomenon in which cognitive performance is compromised when individuals are reminded that they belong to a social group with a negative stereotype related to the cognitive domain in which individual must perform in) consistently finds that stereotype threat reduces performance because it exhausts CWM resources, presumably directly (Beilock, Rydell, & McConnell, 2007). Yet, the present neuroimaging results hint to an alternative possibility. Managing stereotypes in mind may engage SWM, which Studies 1 and 2 showed increases both the lateral frontoparietal and mentalizing systems. Indeed, basic (non-effortful) forms of stereotype processing have been shown to activate the mentalizing system (Contreras et al., 2012). Importantly, cognitive performance in domains studied in the context of stereotype threat (e.g., math performance) not
only require the lateral frontoparietal system to increase but also the mentalizing system to simultaneously decrease (McKiernan et al., 2003). Thus, it is possible that increasing mentalizing regions to manage the social cognitive demands related to stereotypes is what thwarts cognitive performance, as this network needs to be suspended to perform well during non-social reasoning. This would still reduce performance on working memory processes measured in past studies, but via different mechanisms than currently considered. Future work should be able to test this alternative explanation, and depending on results, may lead to novel hypotheses about how to improve cognitive performance while under stereotype threat.

The third contribution of these studies is that, in addition to highlighting basic differences between SWM and CWM mechanisms, they also highlight surprising similarities between SWM and CWM function. That is, in the context of social cognition, the mentalizing system shows very similar functional properties as those systems supporting CWM (i.e., linear increases in activation as a function of load). Moreover, just as CWM training has been shown to improve cognitive reasoning, Study 3 showed that SWM training can improve social cognitive reasoning. Thus, even though SWM relies on at least partially unique underlying mechanisms, these mechanisms’ functional properties might be quite similar to those supporting CWM. Considering other ways in which SWM may function analogously to CWM, as well as nailing down the boundary conditions of this parallel, may lead to otherwise unexamined hypotheses of the mechanisms underlying social cognition. For example, given that managing new information in CWM relates to long-term memory for that information (Oztekin et al., 2010), do different strategies engaged to manage new social information in SWM relate to the kinds of impressions we form of others? And if so, is this phenomenon preferentially mediated by the mentalizing system?
In addition to these contributions, results from Studies 1-3 potentially have great translational value for understanding social cognitive deficits in clinical populations. Individuals with schizophrenia, ASD, and social anxiety, show deficits and/or biases in basic social cognitive processes. Importantly, some of these deficits co-occur with executive function deficits, including deficits in CWM (Couture et al., 2006; Goldman-Rakic, 1994), whereas others occur relatively independently of executive functions like CWM (Ozonoff et al., 2001; Amir et al., 2011). It is possible that including SWM paradigms in the study of these populations may clarify the nature of their social cognitive challenges, as well as the extent to which they are mediated through the mentalizing or lateral frontoparietal system, or the communication between the two. In fact, to my knowledge, no prior paradigms examining social cognitive ability in clinical populations parametrically manipulate various dimensions of social-cognitive information processing (e.g., the number of minds, groups of people, or types of social relationships considered). Meanwhile, the extant conclusions from the neuroimaging literature on the neural basis of social cognitive deficits in clinical disorders are inconclusive. SWM paradigms that, for example, parametrically vary different elements of social information to be managed in mind, may reveal useful neural biomarkers of precise mechanisms driving social cognitive deficits across various clinical populations. Moreover, SWM training and/or SWM + CWM training (depending on whether populations have differential or dual deficits in social cognition and CWM) may help improve social cognitive ability in these populations.

Together, results from this dissertation offer the first insight into the basic mechanisms supporting social working memory. It is my hope that these findings not only paint a more complete picture of everyday social cognitive processing, but in the future may also help those suffering from social cognitive deficits.
References for Introduction and Conclusions


doi:10.1111/j.1467-7687.2009.00848.x


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