NeuroImage 70 (2013) 233–239

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Working memory for social information: Chunking or domain-specific buffer?

Mark A. Thornton *, Andrew R.A. Conway

Princeton University, Department of Psychology, Green Hall, Princeton, NJ 08544, USA

ARTICLE INFO

Article history:
Accepted 17 December 2012
Available online 5 January 2013

Keywords:
Working memory
Social cognition
fMRI
n-back
Chunking

ABSTRACT

Humans possess unique social abilities that set us apart from other species. These abilities may be partially supported by a large capacity for maintaining and manipulating social information. Efficient social working memory might arise from two different sources: chunking of social information or a domain-specific buffer. We test these hypotheses with functional magnetic resonance imaging (fMRI) by manipulating sociality and working memory load in an n-back paradigm. We observe (i) an effect of load in the frontoparietal control network, (ii) an effect of sociality in regions associated with social cognition and face processing, and (iii) an interaction within the frontoparietal network such that social load has a smaller effect than nonsocial load. These results support the hypothesis that working memory is more efficient for social information than for nonsocial information, and suggest that chunking, rather than a domain-specific buffer, is the mechanism of this greater efficiency.

Introduction

Humans make use of a formidable array of cognitive mechanisms to understand the beliefs, desires, intentions, and dispositions of their peers. This understanding makes society and culture possible and helps set us apart from other primate species (Herrmann et al., 2007). Social interactions require us to seamlessly process large quantities of incoming information, combine this input with our preexisting knowledge and beliefs, and produce goal-directed output. In order for any of this to occur in a sensible fashion, we must bear in mind some idea of what other individuals are like and what they are thinking and feeling. In other words, we must form, maintain, and continuously update impressions of others' dispositions and mental states.

The computational demands of social behavior suggest that another highly developed human faculty – working memory – may play a vital role in social cognition. Working memory consists of multiple cognitive mechanisms that allow for the active maintenance and manipulation of information. It allows us to perform mundane tasks such as holding onto a mental image or telephone number, as well as helping us to engage in complex behavior such as reading a book or playing chess (Baddeley and Hitch, 1974; Robbins et al., 1996). Evidence also demonstrates that working memory capacity is strongly correlated with general fluid intelligence (Kane et al., 2005). The cognitive neuroscience of working memory has already been well explored: considerable research points to the critical involvement of a network of frontoparietal regions including lateral prefrontal cortex, anterior cingulate cortex (ACC) and lateral posterior parietal cortex (PPC) (Braver et al., 1997; Chein et al., 2011; Owen et al., 2005; Smith, 2000). Additionally, a number of prefrontal regions have been tied to specific components of working memory specified in the classic theory of Baddeley and Hitch (1974). Dorsolateral prefrontal cortex (DLPFC) has been linked to manipulation of information consistent with central executive function, while more ventral portions of cortex manifest function consistent with domain-specific buffers: the phonological loop and visuospatial sketchpad (D'Esposito et al., 1998). It is worth noting, however, that the notion of domain-specific buffers is not necessary, i.e., mental representations may simply correspond to largely distributed patterns of neural activation (see Postle, 2006).

Despite its central role in higher order cognition, relatively little work has examined the role that working memory per se might play in social cognition and behavior. Although numerous social psychological theories discuss some form of "effortful processing," they rarely go so far as to claim that this means working memory in particular. Indeed, some might argue against the involvement of working memory in social cognition on the basis of phenomenology: social interactions simply seem too easy to require a faculty that we typically associate with difficult tasks. For example, some forms of casual conversation involve shared knowledge, or common ground, which relieves cognitive burden (Nadig and Sedivy, 2002). Another puzzle emerges from the neuroimaging literature, in that the frontoparietal activity seems to generally be anticorrelated with activity in the default network — a set of regions with high resting metabolic activity and a tendency to deactivate relative to baseline during cognitively demanding tasks (Buckner et al., 2008; Raichle et al., 2001). The default network overlaps to a great extent with regions robustly engaged by social cognition such as medial prefrontal cortex (MPFC),

Abbreviations: FMRI, functional magnetic resonance imaging; ACC, anterior cingulate cortex; PPC, posterior parietal cortex; DLPFC, dorsolateral prefrontal cortex; MPFC, medial prefrontal cortex; TPJ, temporoparietal junction; IFG, inferior frontal gyrus; SMA, supplementary motor area; FG, fusiform gyrus; OFC, orbitofrontal cortex.

* Corresponding author at: Harvard University, Department of Psychology, Northwest Science Building 280.14, 52 Oxford Street, Cambridge, MA 02138, USA. Fax: 1-617-495-1492.
E-mail addresses: mthornton@fas.harvard.edu (M.A. Thornton), aconway@princeton.edu (A.R.A. Conway).

1053-8119/$ – see front matter
http://dx.doi.org/10.1016/j.neuroimage.2012.12.063

the temporoparietal junction (TPJ) and medial PPC (Buckner and Carroll, 2007; Spreng et al., 2009). Thus working memory and social cognition might appear as antagonistic processes at first glance.

Social working memory

A number of studies have attempted to resolve this apparent conflict by shifting working memory into the social domain. Research by Druzgal and D'Esposito (2001, 2003) on working memory for facial identity marks an early foray into this territory. They initially found that working memory load increased activity in fusiform regions long associated with face processing (Kanwisher and Yovel, 2006; Kanwisher et al., 1997) and lateral prefrontal cortex (Druzgal and D'Esposito, 2001). However, upon closer examination they discovered that prefrontal activity tended to be more sustained (characteristic of working memory regions) over a delay period, while fusiform activity was more transient (characteristic of regions accessed during working memory) (Druzgal and D'Esposito, 2003). In another study, LoPresti and colleagues contrasted working memory for facial identity with working memory for emotional expressions (LoPresti et al., 2008). They replicated Druzgal and D'Esposito's earlier finding of transient activity in posterior face processing regions, but also demonstrated sustained activity in more anterior affective processing regions including orbitofrontal cortex (OFC), the amygdala and the hippocampus when participants held emotional face information in mind.

Most recently, Meyer et al. (2012) manipulated working memory load in a task that required reordering friends' names according to social dimensions such as friendliness. They replicated the classic working memory finding of load sensitivity in the frontoparietal network, but critically also observed that activity in social network regions – MPFC, TPJ and precuneus/posterior cingulate cortex – varied parametrically with load. This tantalizing result reverses the typical relationship between these networks and demonstrates that they can indeed function together when circumstances require it.

However, much more remains to be understood about the role of social network regions in working memory. One substantial gap in our knowledge stems from the fact that none of the previous studies have attempted to directly manipulate the sociality of information at the same time as working memory load. Meyer et al., the group that makes the strongest argument for social specificity, argue that the existing neuroimaging literature on working memory serves as an implicit control for their experiment. While this might be justifiable with regards to their primary finding – the effect of load within social regions – this approach leaves them unable to answer specific questions regarding the interaction between sociality and load. Most importantly, Meyer et al.'s study could not answer a fundamental question about social working memory: whether it taxes the classical working memory regions of the frontoparietal control network less so than a nonsocial control.

Efficiency hypotheses

The current study aims to fill this gap in the literature by directly manipulating both sociality and load within a single fMRI experiment. By doing so, we aim to determine two things: whether working memory for social information burdens the frontoparietal network less than working memory for comparable nonsocial information, and if so, whether this facilitation results from efficient chunking of social information or a domain-specific buffer.

The two theories being tested merit further explanation. The chunking hypothesis is based upon the well-known process of chunking, in which perceptual systems group associated low-level information into high level chunks (Gobet et al., 2001). It is important to note that chunking may occur as a deliberate retrieval strategy or as an automatic process, with the transition to automaticity mediated by practice. Given the high degree of familiarity people have with faces, we use chunking to refer to the automatic process throughout the paper. Druzgal and D'Esposito (2003) actually suggested the use of chunking in working memory for facial identity, and from there the extension to other social dimensions of faces and social information more generally is a relatively short one. By preprocessing – i.e. chunking – we may be able to reduce the complex sensory correlates of social data down to much more manageable representations of social information. Given the large number of facial features related to perceptions of trustworthiness (Oosterhof and Todorov, 2008), the reduction of this lengthy visual feature vector to a more manageable social representation may well explain increased efficiency in social working memory.

The buffer hypothesis also originates from classic working memory literature, in particular Baddeley's notion of domain-specific slave systems tied to the central executive. Baddeley and Hitch (1974) originally specified two such systems or buffers, the visuospatial sketchpad and the phonological loop. Later, Baddeley added a third slave system – the episodic buffer (Baddeley, 1992). The buffer hypothesis that we test proposes that people possess a buffer devoted to social information. The existence of such a buffer would allow more social information to be held in mind before overburdening the central executive. The possibility of a social buffer likely never surfaced before because until recently, social information was not considered a truly distinct domain of knowledge. However, the advent of social neuroscience has undermined the idea that social cognition can be explained entirely in terms of domain general cognition mechanisms and generated support for the idea of a sovereign social domain in the brain (Mitchell, 2009). We presume that the non-social control condition in our experiment – which involves spatial locations – makes use of the visuospatial sketchpad.

These two theories make distinct predictions about the behavioral and neural effects of manipulating sociality of information and working memory load. Chunking requires a combination of perceptual resources and executive attention (Bor et al., 2003). Thus, the chunking hypothesis predicts an up-front cost of preprocessing chunks, one that would manifest as a negative main effect of sociality on behavioral performance (that is, slower reaction times to social vs. non-social information) and a positive main effect of sociality on activity in regions associated with social perception. In previous research, regions associated with domain-specific buffers have shown parametric increases in activity in response to load when the relevant type of information was presented (D'Esposito et al., 1998). Thus, the buffer hypothesis predicts an interaction between sociality and load in regions associated with social cognition such that neural activity should scale with load only in the social condition. The result of the research of Meyer et al. (2012) already lends support to this hypothesis, although without the control condition necessary for a direct test of the predicted interaction. The key difference between chunking and buffer hypotheses resides, therefore, within regions activated by the main effect of sociality: the buffer hypothesis predicts a flexible domain-specific resource that scales with load while the chunking hypothesis predicts load-invariant perceptual preprocessing. Of course, consistent with the considerable extant literature, both hypotheses would predict an increase in frontoparietal activity and a decrement in performance with increased load. Finally, the overall hypothesis of efficient social working memory predicts an interaction between sociality and load such that the simple effect of load is smaller within the social condition than within the nonsocial condition in terms of both behavioral performance and neural activity in the frontoparietal network.

Material and methods

Participants

Sixteen participants (10 female, mean age = 22, $SD = 2.3$) were recruited from the Princeton University community. All participants were right-handed, neurologically normal, had normal or corrected-to-normal vision and were fluent in English. Participants provided informed consent in accordance with the regulations of the Princeton University Institutional Review Board and were paid $20.

Stimuli

Stimuli consisted of 55 faces made with FaceGen Modeller (http://facegen.com; Blanz and Vetter, 1999; Singular Inversions, 2006), a software program designed for the creation of realistic 3D images of faces. Each face was randomly generated, subject to the following parameters: European, age 20 to 30, average masculinity/femininity. These faces were manipulated in terms of their perceived trustworthiness through an established model of social face perception (Oosterhof and Todorov, 2008). This model was developed by using principal component analysis to extract the two major dimensions (trustworthiness and dominance) underlying trait inferences from facial appearance, and then using a data driven approach based on 3D scans of real faces to determine which physical aspects of faces correspond to judgments of these dimensions. The practical application of this process was a slider bar in FaceGen that can be used to adjust the degree of trustworthiness people perceive in computer generated faces. For the present study, five faces were morphed to each of 11 levels of trustworthiness ranging from −5 *SD* through +5 *SD*. All images were shown against a black background; inter-stimulus blanks consisted solely of this background. The stimuli were presented with MATLAB® 7 (www.themathworks.com) using the Psychophysics Toolbox 3 extensions (Brainard, 1997; Pelli, 1997). Images were projected onto a screen at the back of the MRI and reflected into participants' eyes via a small mirror mounted on the head coil.

Experimental protocol

The study adhered to a 2 (sociality) × 2 (load) block design. Participants performed a task (Fig. 1) resembling the common n-back working memory paradigm. The experiment consisted of 20 1-min blocks separated evenly into four runs, plus four practice blocks at the beginning of the study. Each block was drawn from one cell in the experimental design: social 1-back (s1), social 2-back (s2), nonsocial 1-back (ns1) or nonsocial 2-back (ns2). Conditions were presented in a different random order for each subject. Within each block, 24 faces were presented in sequence. Faces remained on the screen for 1 s followed by a blank screen for 1 s before the next face appeared. At the end of each block the word “rest” was displayed for 2 s followed by a 6 s break with blank screen.

In all conditions, faces varied in terms of their trustworthiness and their spatial position. Spatial positions consisted of 11 equally-likely locations evenly-spaced along the left–right axis in the middle of the screen. Spatial locations were thus directly analogous to the levels of trustworthiness in face-space. Considerable work suggests that faces and inferred traits can be represented dimensionally, justifying the supposition that information was represented in a similar format in both the social and nonsocial conditions (Oosterhof and Todorov, 2008; Valentine, 1991). For each block, faces and positions were independently randomly sampled without replacement from the pools of faces and analogous spatial positions.

The participant's goal depended on the instruction at the beginning of each block. In the nonsocial blocks, participants were instructed to focus on the spatial location of each face. On each trial, they were asked to press the right button if the current face was to the right of the face n-back and to press the left button if the current face was to the left of the face n-back. In the social blocks, participants were instructed to focus on the trustworthiness of each face. They were asked to press the right button if the current face was more trustworthy than the face n-back or to press the left button if the current face was less trustworthy than the face n-back. Responses and reaction times were recorded via a button box in the participant's right hand. Faces were prevented from matching the item 1 or 2-back in terms of trustworthiness or position in order to ensure that there was always an appropriate response to each item. No response was required on the first one or two trials (depending on condition), as there were no faces n-back from these trials.

Imaging procedure

Imaging was performed on a Siemens 3.0 T Allegra head-only scanner (Siemens, Erlangen, Germany) with standard head coil. A high-resolution 3D anatomical (T1) image was acquired at the beginning of each scan (TR = 2500 ms, TE = 4.38 ms, flip angle = 8°, matrix size = 256 × 256, 176 sagittal slices). Functional echo planar images (EPIs) were obtained from the whole brain using 34 interleaved axial slices of 3 mm thickness and 1 mm spacing (TR = 2000 ms, TE = 30 ms, flip angle = 75°, matrix size = 64 × 64, 150 measurements per run).

Preprocessing and analysis of MRI data took place in SPM8 (Wellcome Department of Cognitive Neurology, London, United Kingdom). Data were spatially realigned and unwarped to correct for head motion. Images were then normalized to a standard anatomical space (2 mm isotropic voxels) on the basis of the ICBM 152 brain template (Montreal Neurological Institute [MNI]). Normalized images were spatially smoothed with a 6 mm FWHM Gaussian kernel.

Preprocessed data were analyzed with the general linear model. Boxcar regressors for each of the four block types were convolved with a canonical hemodynamic response function and combined with additional nuisance regressors (head motion, session mean, linear trends and temporal and dispersion derivatives) to model the data. Each subject was analyzed separately in order to generate beta maps of the conditions

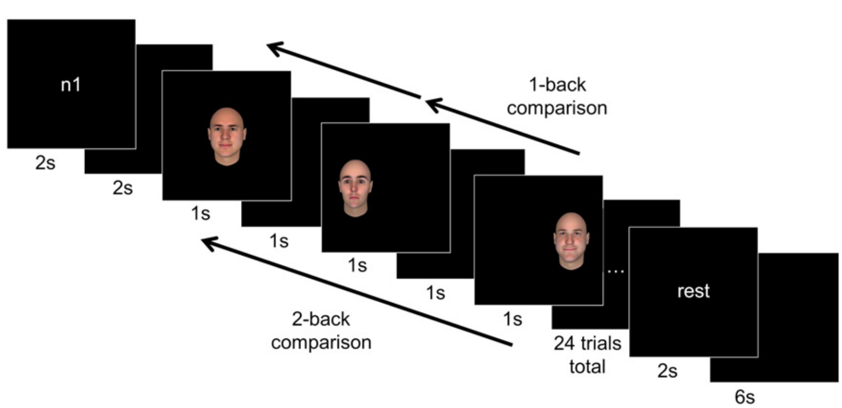

Fig. 1. Working memory task. This schematic illustrates the protocol for a single block. Participants attended to faces' locations in the nonsocial conditions and their trustworthiness in the social conditions, making comparative responses to the face n-back on each trial.

of interest for entry into a second-level analysis. This analysis consisted of a voxel-wise 2×2 repeated-measures analysis of variance (ANOVA). An experiment-wise statistical threshold of $p<.05$ was obtained via a cluster correction method (Slotnick et al., 2003) with a voxel-wise threshold of $p<.001$ and cluster threshold of 23 contiguous resampled voxels. Results were visualized on the cortical surface with Caret (http://www.nitrc.org/projects/caret/) (Van Essen et al., 2001).

Results

Two participants were excluded from analyses: one due to excessive head motion and the other due to self-reported failure to comply with directions in the behavioral task. One participant reversed button responses and was therefore reverse-scored. Thus, imaging analyses included 14 participants (9 female, mean age = 22, $SD = 2.45$). Due to an equipment error, behavioral responses from one of these participants were not recorded.

Behavioral data

Participant accuracy and reaction times were analyzed in SPSS® 19. For all null hypothesis significance tests, $\alpha = 0.05$ and effect sizes were calculated using the formula for partial eta-squared (η^2_p). Accuracy and reaction time were aggregated by condition (Table 1). Since participants varied substantially in terms of their overall tendency to respond, no-response trials were excluded from analysis.

A two-way within-subjects ANOVA on accuracy yielded a significant interaction between sociality and load, $F(1,12) = 5.82$, $p<.05$, $\eta^2_p = .33$. Overall accuracy for the social condition was lower than for the nonsocial condition, $F(1,12) = 24.16$, $p<.001$, $\eta^2_p = .688$, but these conditions are not directly comparable because trustworthiness judgments are inherently subjective and accuracy in the social condition merely represents consistency with the model of Oosterhof and Todorov (2008) rather than objective fact. Simple effects analyses of load revealed that accuracy declined as a function of load in both social, $F(1,12) = 9.98$, $p<.01$, $\eta^2_p = .45$, and nonsocial, $F(1,12) = 13.93$, $p<.005$, $\eta^2_p = .54$, conditions. The slightly larger effect of load in the nonsocial condition relative to the social condition is consistent with the general prediction of facilitated social working memory.

An identical analysis was undertaken with regard to reaction time. Again there was a significant interaction between sociality and load, $F(1,12) = 19.95$, $p<.001$, $\eta^2_p = .62$, and a main effect of sociality, $F(1,12) = 29.23$, $p<.001$, $\eta^2_p = .71$. Unlike the un-interpretable main effect of sociality on “accuracy,” the difference in reaction times can be interpreted as support for the chunking hypothesis's prediction of greater preprocessing of social information. Simple effects analyses revealed significant increases in reaction time as a function of higher load for both the social, $F(1,12) = 6.82$, $p<0.05$, $\eta^2_p = .36$, and nonsocial conditions, $F(1,12) = 28.10$, $p<.001$, $\eta^2_p = .70$. Again, the fact that the effect of social load was smaller than the effect of nonsocial load supports the general hypothesis of facilitated social working memory.

Unlike the typical n-back task, participants could have performed above-chance on the current task without actually holding items in memory. Namely this may be achieved by evaluating each face's position or trustworthiness and pressing the right button if they are more trustworthy or further right than the average face and pressing the left button if the converse is true. The possibility of cheating stemmed from the use of dimensions rather than categories in the memory task; we accepted this drawback because we anticipated that dimensions would minimize the possibility of differential verbal coding between conditions.

Participants did not report such cheating behavior, but to address this possibility we conducted a binomial regression of accuracy onto item difficulty within each subject. Difficulty was calculated by taking the absolute value of the difference between a trial's trustworthiness or position (depending on condition) and the trustworthiness or position of the trial n-back. This value was then subtracted from 10 to give a difficulty score (with 9 being most difficult and 0 least difficult). Since this difficulty measure indexes only to the task difficulty and not to the difficulty of cheating, participants' accuracy should be negatively related with difficulty if and only if they are actually performing the task.

Due to the paucity of errors in the nonsocial conditions, the regression failed to converge for five participants in the ns1 condition and one participant in the ns2 condition. Considering the 12 participants with valid regression coefficients in the ns2, s1 and s2 conditions revealed that 100% of these coefficients were negative ($M = -.27$), thus strongly indicating that higher difficulty was associated with significantly lower probability of accuracy. Paired t-tests indicated that the average coefficient did not significantly differ among these three conditions. Although these analyses do not entirely rule out cheating, they do suggest that participants were actually performing the task and did not appear to cheat differentially across conditions.

Table 1
Accuracy and reaction time by condition.[a]

	Accuracy (proportion correct)				Reaction time (seconds)			
Condition	ns1	ns2	s1	s2	ns1	ns2	s1	s2
Mean	0.96	0.82	0.73	0.70	0.63	0.87	0.92	0.97
SD	0.06	0.11	0.08	0.08	0.13	0.15	0.11	0.11

[a] Accuracy for social conditions reflects model consistency.

Imaging data

Analysis of the functional neuroimaging data revealed significant main effects of sociality and load as well as an interaction between them (Fig. 2). As predicted by both the buffer and chunking hypotheses – as well as previous neuroimaging work – the main effect of load activated an extended frontoparietal network. This activation included DLPFC, premotor cortex, the posterior inferior frontal gyrus (pIFG), ACC/supplementary motor area (SMA), lateral and medial PPC, and several other regions (Table 2). Although in almost all cases the main effect of load corresponded to an increase in BOLD activity, the one noticeable exception was the deactivation of two portions of medial OFC (Fig. 2). This decrease in activity is consistent with earlier default network findings.

Consistent with both buffer and chunking hypotheses, the main effect of sociality activated a number of regions previously associated with face perception and social and affective processing. These regions included the fusiform gyrus (FG), anterior inferior frontal gyrus (aIFG) and lateral OFC, as well as a number of other regions (Table 3). Although the main effect of sociality generated several trending activations in MPFC, none of these survived the statistical threshold and cluster correction. Curiously, a portion of the precuneus actually manifested a main effect of sociality corresponding to less activity in the social condition than the nonsocial condition. Contrary to the predictions of the buffer hypothesis – as well as some earlier findings – we found no evidence of load effects within most portions of the network activated by sociality. Indeed, there were only two small regions of overlap between the main effects of load and sociality: one in left DLPFC and another in the portion of the precuneus that was less active in the social condition.

The observed interaction between sociality and load took place in a subset of the frontoparietal control network largely overlapping with the main effect of load. Regions manifesting the interaction included the pIFG, SMA, and lateral PPC, among others (Table 4). Consistent with the general prediction of facilitated social working memory, the effect of social load was smaller than the effect of nonsocial load in these regions (Fig. 2). Inconsistent with the buffer hypothesis, there was no interaction in social regions such that they manifested an effect of load more strongly in the social condition.

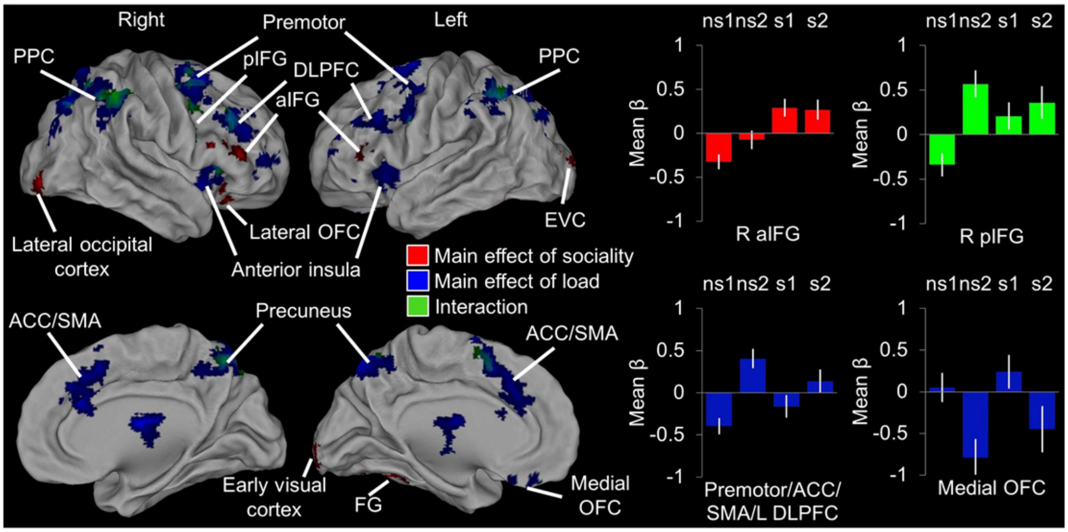

Fig. 2. Two-way repeated-measures ANOVA. Graphs illustrate patterns of neural responses in regions activated by sociality (red), working memory load (blue), and their interaction (green). Mean regression coefficients are given for nonsocial 1-back (ns1), nonsocial 2-back (ns2), social 1-back (s1) and social 2-back (s2) conditions (error bars +/− 1 *SE*).

Discussion

It might seem strange to claim facilitation of working memory for social information given the worse performance in the social conditions across the board. Indeed, even in most regions showing the facilitation interaction, s1 activity appeared at least somewhat higher than that in ns1. However, it should be emphasized again that these observations are actually predicted by the chunking hypothesis as markers of the up-front cost of efficient social encoding. In previous research, greater activity in frontoparietal regions has been associated with chunking independent of load (Bor et al., 2003). Moreover, the high ratio of updating to maintenance in our paradigm may have emphasized encoding costs and minimized the potential impact of greater efficiency of storage for large numbers of items. Thus the only valid indicators of working memory burden are the relative sizes of load effects within the social and nonsocial conditions.

The slower responses in the social condition might also be viewed as somewhat puzzling in light of research on the rapid nature of impression formation (Willis and Todorov, 2006), but it should be noted that these studies have not compared faces to a matched control condition as we did in this study. From an information theoretical point of view, it seems unlikely that processing a much more complicated stimulus (a face) could be faster than processing a simpler one (a spatial location), even with dedicated neural machinery. Moreover such effects may be exaggerated under cognitive load. Still, we cannot entirely rule out the possibility that the inherently subjective nature of social judgments also contributed to the behavioral delay.

There are a number of discrepancies between the current results and earlier investigations of this topic that require further consideration. One puzzle is that unlike initial research on working memory for faces that also employed an n-back paradigm (Druzgal and D'Esposito, 2001), we did not observe an effect of load in regions associated with face processing. There are two likely explanations for this. One possibility suggested by earlier work (LoPresti et al., 2008) is that working memory for social information per se may require less maintenance of visual imagery in high-level vision areas than working memory for facial identity. However, this might not explain the absence of load effect in most prefrontal social regions. Another possibility is that the task employed here may have been better than a normal n-back or a delayed-match-to-sample task in eliciting only sustained activity while ignoring transient activity. It should

Table 2
Peak voxel and cluster size for all regions obtained from the main effect of sociality ($p<0.05$, corrected).[a]

Anatomical label	x	y	z	Volume	Max F
Cerebellum	58	−59	−34	31	32.86
	38	−37	−32	78	30.35
	−26	−85	−24	230	96.48
Cerebellum/FG	−32	−69	−20	27	32.19
FG	−40	−55	−20	171	123.95
aIFG	56	21	16	292	94.40
	−52	39	14	134	55.71
aIFG/temporal pole	−46	21	−22	40	33.57
Lateral occipital cortex	40	−87	−8	466	95.84
	−34	−99	−12	64	38.69
Early visual cortex	−6	−107	2	411	78.40
	10	−105	12	68	40.84
Lateral OFC	22	31	−18	170	61.23
	44	29	−8	40	45.04
Precuneus	2	−63	62	65	58.27
DLPFC	−30	54	20	30	32.88

[a] The main effect corresponded to greater activity in the social condition than the nonsocial condition in all regions except the precuneus, which showed the reverse. Coordinates refer to MNI stereotaxic space.

Table 3
Peak voxel and cluster size for all regions obtained from the main effect of working memory load ($p<0.05$, corrected).[a]

Anatomical label	x	y	z	Volume	Max F
Anterior insula	−30	17	2	785	56.76
Anterior insula/thalamus	6	−7	14	2500	102.90
Cerebellum	−34	−37	−42	84	48.10
	8	−77	−32	171	58.39
	38	−65	−34	281	46.29
	−36	−67	−34	268	37.85
	−24	−19	−38	34	45.93
	−62	−63	−42	23	33.07
	−20	−81	−28	50	29.26
Medial OFC	−4	39	−24	46	23.27
	−4	27	−22	26	24.86
Medulla	2	−39	−48	32	28.59
Posterior cingulate cortex	18	−37	40	45	31.27
PPC	−8	−71	58	6927	87.92
Premotor cortex/ACC/DLPFC	−30	1	62	8050	103.92
DLPFC	−54	41	−8	24	29.98

[a] The main effect corresponded to greater activity in the 2-back condition than the 1-back condition in all regions except medial orbitofrontal cortex, which showed the reverse. Coordinates refer to MNI stereotaxic space.

Table 4
Peak voxel and cluster size for all regions obtained from the interaction between sociality and working memory load ($p<0.05$, corrected).[a]

Anatomical label	x	y	z	Volume	Max F
Anterior Insula	32	25	0	59	40.28
Cerebellum	34	−41	−48	25	24.90
pIFG	−40	1	34	83	35.17
	50	9	36	473	112.97
DLPFC	40	33	38	152	41.36
	−52	33	42	105	41.53
	28	9	50	400	40.85
PPC	32	−69	42	1813	77.36
	−38	−49	50	563	56.59
	−36	−31	38	32	27.57
Precuneus	−10	−59	58	36	24.01
Sub-gyral parietal lobe	−26	−59	24	44	30.15
SMA	−8	11	52	90	32.81

[a] The interaction corresponded to a smaller simple effect of load in the social condition than the nonsocial condition in all regions. Coordinates refer to MNI stereotaxic space.

be pointed out that unlike the typical n-back, participants in this study made a forced choice comparison on every trial rather than just occasionally indicating matching identity, which may have forced them into a more active strategy that emphasized sustained neural activations.

The set of regions activated by the sociality manipulation in this experiment differ substantially from those emphasized in earlier studies of social cognition (Amodio and Frith, 2006; Mitchell et al., 2002, 2005; Rilling et al., 2004; Saxe and Kanwisher, 2003; Saxe and Wexler, 2005). Notably absent in the results reported here are MPFC, medial PPC, and the TPJ. However, the default network is represented by the temporal pole – a region associated with social semantic knowledge (Ross and Olson, 2009; Zahn et al., 2007) – and aIFG (*pars triangulum*). Although these regions may be peripheral to the largely midline default network, they do demonstrate strong resting-state functional connectivity with the better known regions (Yeo et al., 2011). Although not part of the default network, lateral OFC also has a well-established role in processing emotional stimuli (Bechara et al., 2000; Blair et al., 1999). The differences in social activations are not particularly worrisome considering evidence that different systems may bear responsibility for processing social information from different sensory modalities (Waytz and Mitchell, 2011; Zaki et al., 2010).

Given our assumption that the nonsocial condition was supported by the visuospatial sketchpad, it might have been worrying if any of our effects had been limited to right ventrolateral prefrontal cortex since this region has been implicated in specifically visual working memory (D'Esposito et al., 1998). Such localization might have suggested that effects were being driven by differences in the extent to which the visuospatial sketchpad was employed, rather than anything to do with sociality per se. Fortunately, the widespread, bilateral nature of both of the main effects and the interaction ameliorate this concern.

In Meyer et al.'s (2012) investigation of social working memory, regions including MPFC and the precuneus manifested increased activity in response to social working memory load. However, several of the putatively social regions observed by Meyer et al. during the delay period of their experiment actually appear to overlap considerably with regions which show a main effect of load (and not sociality) in our experiment. Since they did not manipulate the sociality of information, it is difficult to be sure which of the midline activations in their experiment originate within default network regions and which originate in nearby frontoparietal regions such as the ACC. They attempted to address this issue by identifying regions that showed both a parametric effect of load and a correlation with trait perspective-taking across subjects. However this analysis produced only ventral portions of MPFC and medial parietal cortex, suggesting that load sensitivity attributed to dorsal MPFC and the TPJ may in fact originate in adjacent frontoparietal regions. However, as far as ventral MPFC and the precuneus are concerned, discrepancies between our findings and theirs are probably best explained by substantial differences in the processing demand of our social tasks: it is entirely possible that the social network regions observed in our experiment might express different working memory properties than those within the core default network. Indeed some evidence has already been produced for that hypothesis (Spunt and Lieberman, 2013).

Conclusions

The results of this experiment support the idea of facilitated working memory for social information and suggest that this facilitation may occur due to efficient chunking rather than a domain-specific social buffer. Behaviorally, participants demonstrated worse performance on a working memory task under high load than load low. However, as predicted, this main effect of load was qualified by an interaction such that the decrement of load was smaller for social information. Slower reaction times in the social condition than the nonsocial condition may result from the substantial up-front cost of preprocessing predicted by the chunking hypothesis. In the brain, working memory load activated an extended frontoparietal control network while deactivating portions of the default network. Consistent with the general prediction of facilitated social working memory, portions of the frontoparietal network manifested an interaction such that the effect of load was smaller in the social condition. Contrary to the buffer hypothesis and supporting the chunking hypothesis, a number of regions involved in social processing became more active in the social condition but showed no simple effect of social load. It should be emphasized just how surprising this finding is: it suggests that the chunking of social information is so efficient that maintaining a representation of the trustworthiness an additional face actually requires fewer executive resources than maintaining an additional nonsocial representation as simple as a location on a line.

Future directions

The evidence presented here suggests that the brain may facilitate the process of maintaining and updating social information by preprocessing it into efficient chunks. This result may help us understand why humans appear to possess such unique social gifts. Down the road it may also provide a new avenue for understanding the dysfunction of normal social cognition in disorders such as autism and schizophrenia. However at present much remains to be discovered about the interactions between social cognition and working memory.

Furthermore, although we do not find support for the idea here, the notion of a social buffer is worthy of further investigation. The results of Meyer et al. (2012) suggest such a buffer, at least within a more verbal domain of social processing. One possibility worthy of consideration is that this buffer is actually identical to the episodic buffer in Baddeley's model. The default network is known to be involved in a wide-range of self-projecting tasks, including episodic past and future thinking and perspective-taking (Buckner and Carroll, 2007). Almost all of these tasks involve a social element: episodic memory for source memory, episodic future thinking for simulating future interactions, and perspective taking for mentalizing. Thus, it may well be that a part of the default network serves as the episodic or social buffer.

Acknowledgments

The authors would like to thank Daniel L. Ames, Sean Baron, and Jason Mitchell for their assistance with this research and manuscript. This work was conducted in fulfillment of thesis requirement of Princeton University, and was partially supported by the Office of the Dean of the College.

References

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277.
Baddeley, A.D., 1992. Working memory. Science 255, 556–559.
Baddeley, A.D., Hitch, G., 1974. Working memory. In: Gordon, H.B. (Ed.), Psychology of Learning and Motivation, vol. 8. Academic Press, pp. 47–89.
Bechara, A., Damasio, H., Damasio, A.R., 2000. Emotion, decision making and the orbitofrontal cortex. Cereb. Cortex 10, 295–307.
Blair, R.J.R., Morris, J.S., Frith, C.D., Perrett, D.I., Dolan, R.J., 1999. Dissociable neural responses to facial expressions of sadness and anger. Brain 122, 883–893.
Blanz, V., Vetter, T., 1999. A morphable model for the synthesis of 3d faces. Proc. ACM SIGGRAPH Conf. computer graph, 26, pp. 187–194.
Bor, D., Duncan, J., Wiseman, R.J., Owen, A.M., 2003. Encoding strategies dissociate prefrontal activity from working memory demand. Neuron 37, 361–367.
Brainard, D.H., 1997. The psychophysics toolbox. Spat. Vis. 10, 433–436.
Braver, T.S., Cohen, J.D., Nystrom, L.E., Jonides, J., Smith, E.E., Noll, D.C., 1997. A parametric study of prefrontal cortex involvement in human working memory. NeuroImage 5, 49–62.
Buckner, R.L., Carroll, D.C., 2007. Self-projection and the brain. Trends Cogn. Sci. 11, 49–57.
Buckner, R.L., Andrews-Hanna, J.R., Schacter, D.L., 2008. The brain's default network. Ann. N. Y. Acad. Sci. 1124, 1–38.
Chein, J.M., Moore, A.B., Conway, A.R.A., 2011. Domain-general mechanisms of complex working memory span. NeuroImage 54, 550–559.
D'Esposito, M., Aguirre, G.K., Zarahn, E., Ballard, D., Shin, R.K., Lease, J., 1998. Functional MRI studies of spatial and nonspatial working memory. Cogn. Brain Res. 7, 1–13.
Druzgal, T.J., D'Esposito, M., 2001. Activity in fusiform face area modulated as a function of working memory load. Cogn. Brain Res. 10, 355–364.
Druzgal, T.J., D'Esposito, M., 2003. Dissecting contributions of prefrontal cortex and fusiform face area to face working memory. J. Cogn. Neurosci. 15, 771–784.
Gobet, F., Lane, P.C.R., Croker, S., Cheng, P.C.H., Jones, G., Oliver, I., Pine, J.M., 2001. Chunking mechanisms in human learning. Trends Cogn. Sci. 5, 236–243.
Herrmann, E., Call, J., Hernandez-Lloreda, M.V., Hare, B., Tomasello, M., 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. Science 317, 1360–1366.
Kane, M.J., Hambrick, D.Z., Conway, A.R.A., 2005. Working memory capacity and fluid intelligence are strongly related constructs: comment on Ackerman, Beier, and Boyle (2005). Psychol. Bull. 131, 66–71.
Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. Philos. Trans. R. Soc. Lond. B Biol. Sci. 361, 2109–2128.
Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.
LoPresti, M.L., Schon, K., Tricarico, M.D., Swisher, J.D., Celone, K.A., Stern, C.E., 2008. Working memory for social cues recruits orbitofrontal cortex and amygdala: a functional magnetic resonance imaging study of delayed matching to sample for emotional expressions. J. Neurosci. 28, 3718–3728.
Meyer, M.L., Spunt, R.P., Berkman, E.T., Taylor, S.E., Lieberman, M.D., 2012. Evidence for social working memory from a parametric functional MRI study. Proc. Natl. Acad. Sci. U. S. A. 109, 1883–1888.
Mitchell, J.P., 2009. Social psychology as a natural kind. Trends Cogn. Sci. 13, 246–251.
Mitchell, J.P., Heatherton, T.F., Macrae, C.N., 2002. Distinct neural systems subserve person and object knowledge. Proc. Natl. Acad. Sci. U. S. A. 99, 15238–15243.
Mitchell, J.P., Macrae, N.C., Banaji, M.R., 2005. Forming impressions of people versus inanimate objects: social-cognitive processing in the medial prefrontal cortex. NeuroImage 26, 251–257.
Nadig, A.S., Sedivy, J.C., 2002. Evidence of perspective-taking constraints in children's on-line reference resolution. Psychol. Sci. 13, 329–336.
Oosterhof, N.N., Todorov, A., 2008. The functional basis of face evaluation. Proc. Natl. Acad. Sci. U. S. A. 105, 11087–11092.
Owen, A.M., McMillan, K.M., Laird, A.R., Bullmore, E., 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. Hum. Brain Mapp. 25, 46–59.
Pelli, D.G., 1997. The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vis. 10, 437–442.
Postle, B.R., 2006. Working memory as an emergent property of the mind and brain. Neuroscience 139, 23–38.
Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. U. S. A. 98, 676–682.
Rilling, J.K., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2004. The neural correlates of theory of mind within interpersonal interactions. NeuroImage 22, 1694–1703.
Robbins, T., Anderson, E., Barker, D., Bradley, A., Fearnyhough, C., Henson, R., Hudson, S., Baddeley, A., 1996. Working memory in chess. Mem. Cognit. 24, 83–93.
Ross, L.A., Olson, I.R., 2009. Social cognition and the anterior temporal lobes. NeuroImage 49, 3452–3462.
Saxe, R., Kanwisher, N., 2003. People thinking about thinking people: the role of the temporo-parietal junction in "theory of mind". NeuroImage 19, 1835–1842.
Saxe, R., Wexler, A., 2005. Making sense of another mind: the role of the right temporo-parietal junction. Neuropsychologia 43, 1391–1399.
Singular Inversions, 2006. Facegen 3.1 full software development kit documentation.
Slotnick, S.D., Moo, L.R., Segal, J.B., Hart, J., 2003. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. Cogn. Brain Res. 17, 75–82.
Smith, E.E., 2000. Neural bases of human working memory. Curr. Dir. Psychol. Sci. 9, 45–49.
Spreng, R.N., Mar, R.A., Kim, A.S.N., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. 21, 489–510.
Spunt, R.P., Lieberman, M.D., 2013. The busy social brain: Evidence for automaticity and control in the neural systems supporting social cognition and action understanding. Psychol. Sci. 24, 80–86.
Valentine, T., 1991. A unified account of the effects of distinctiveness, inversion, and race in face recognition. Q. J. Exp. Psychol. A 43, 161–204.
Van Essen, D.C., Drury, H.A., Dickson, J., Harwell, J., Hanlon, D., Anderson, C.H., 2001. An integrated software suite for surface-based analyses of cerebral cortex. J. AHIMA 8, 443–459.
Waytz, A., Mitchell, J.P., 2011. Two mechanisms for simulating other minds: dissociations between mirroring and self-projection. Curr. Dir. Psychol. Sci. 20, 197–200.
Willis, J., Todorov, A., 2006. First impressions: making up your mind after a 100-ms exposure to a face. Psychol. Sci. 17, 592–598.
Yeo, B.T.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., Roffman, J.F., Smoller, J.W., Zöllei, L., Polimeni, J.R., Fischl, B., Liu, H., Buckner, R.L., 2011. The organization of the human cerebral cortex estimated by functional connectivity. J. Neurophysiol. 106, 1125–1165.
Zahn, R., Moll, J., Krueger, F., Huey, E.D., Garrido, G., Grafman, J., 2007. Social concepts are represented in the superior anterior temporal cortex. Proc. Natl. Acad. Sci. U. S. A. 104, 6430–6435.
Zaki, J., Hennigan, K., Weber, J., Ochsner, K.N., 2010. Social cognitive conflict resolution: contributions of domain-general and domain-specific neural systems. J. Neurosci. 30, 8481–8488.