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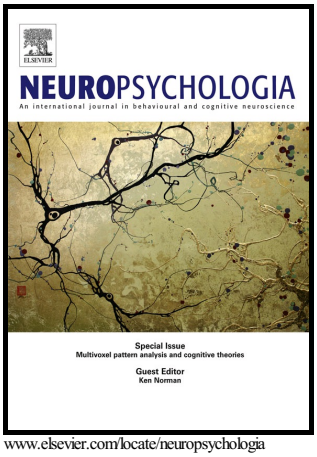

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Should I trust you? Learning and memory of social interactions in dementia

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Abstract

Social relevance has an enhancing effect on learning and subsequent memory retrieval. The ability to learn from and remember social interactions may impact on susceptibility to financial exploitation, which is elevated in individuals with dementia. The current study aimed to investigate learning and memory of social interactions, the relationship between performance and financial vulnerability and the neural substrates underpinning performance in 14 Alzheimer's disease (AD) and 20 behavioural-variant frontotemporal dementia (bvFTD) patients and 20 age-matched healthy controls. On a "trust game" task, participants invested virtual money with counterparts who acted either in a trustworthy or untrustworthy manner over repeated interactions. A non-social "lottery" condition was also included. Participants' learning of trust/distrust responses and subsequent memory for the counterparts and nature of the interactions was assessed. Carer-rated profiles of financial vulnerability were also collected. Relative to controls, both patient groups showed attenuated learning of trust/distrust responses, and lower overall memory for social interactions. Despite poor learning performance, both AD and bvFTD patients showed better memory of social compared to non-social interactions. Importantly, better memory for social interactions was associated with lower financial vulnerability in AD, but not bvFTD. Learning and memory of social interactions was associated with medial temporal and temporoparietal atrophy in AD, whereas a wider network of frontostriatal, insular, fusiform and medial temporal regions was implicated in bvFTD. Our findings suggest that although social relevance influences memory to an extent in both AD and bvFTD, this is associated with vulnerability to financial exploitation in AD only, and is underpinned by changes to different neural substrates. Theoretically, these findings provide novel insights into potential mechanisms that give rise to vulnerability in people with dementia, and open avenues for possible interventions.

Keywords: Alzheimer's disease; frontotemporal dementia; memory; social cognition; trust game; financial exploitation

Highlights:

- Susceptibility to financial exploitation is elevated in individuals with dementia
- Learning and memory of social interactions may impact on financial exploitation
- Learning and memory of social interactions were affected in bvFTD and AD
- Memory of social interactions related to financial exploitation in AD only
- Social learning and memory relates to divergent neural substrates in bvFTD and AD

1. Introduction

In everyday life, we draw upon memories of past social experiences to guide current or future social interactions. These include memories of the people with whom we have interacted, and whether these interactions led to socially rewarding outcomes, such as approval, acceptance and reciprocity (Fareri & Delgado, 2014). Converging evidence from neuroimaging studies in healthy adults implicates a network of frontostriatal and medial temporal lobe (MTL) regions, pointing to the involvement of both social reward processing and memory functions to support socially relevant memories (Delgado, Frank, & Phelps, 2005; Tsukiura & Cabeza, 2008; Vrtička, Andersson, Sander, & Vuilleumier, 2009). In healthy older adults, increased susceptibility to financial exploitation is associated with memory decline (James, Boyle, & Bennett, 2014). Although such mistreatment is commonly reported across a range of neurodegenerative conditions, it is unclear whether financial vulnerability is related to impaired memory for social interactions in people with dementia.

Here, we focus on behavioural-variant frontotemporal dementia (bvFTD) and Alzheimer's disease (AD). Patients with bvFTD show progressive changes in personality and social interactions, with disturbance in emotion processing (Kumfor, Irish, Hodges, & Piguet, 2013a), empathy (Dermody *et al.*, 2016), Theory of Mind (Le Bouc *et al.*, 2012), social reward processing and decision making (Grossman et al., 2010; Perry, Sturm, Wood, Miller, & Kramer, 2015), compliance with social norms (O'Callaghan *et al.*, 2016) and strategic social bargaining (Melloni *et al.*, 2016). Of particular relevance, overly friendly or gullible behaviours are frequently reported in bvFTD (Pressman & Miller, 2014), suggesting distinct alterations in processing socially relevant information. Episodic memory impairments in bvFTD can be commensurate with those seen in AD (Hornberger, Piguet, Graham, Nestor, & Hodges, 2010; Pennington, Hodges, & Hornberger, 2011). Notably, in AD socio-emotional

functions remain relatively intact, particularly during the mild-moderate stages of the disease (Bertoux, de Souza LC, et al., 2015a; Shany-Ur & Rankin, 2011). The divergent patterns of social-emotional dysfunction in bvFTD and AD reflect underlying differences in brain regions that are affected in each syndrome, with selective vulnerability of frontostriatal and insular regions in bvFTD, versus MTL and parietal regions in AD (Landin-Romero et al., 2017; Seeley et al., 2007). Nevertheless, it remains unclear how this frontostriatal-insular versus MTL-parietal dissociation potentially disrupts learning and memory of social interactions in these syndromes.

The trust game, an experimental paradigm drawn from the neuroeconomics literature, offers a means of assessing learning and memory for social reciprocity (Johnson & Mislin, 2011; Tzieropoulos, 2013). Originally developed by Berg, Dickhaut and McCabe (1995), the trust game involves an exchange where the participant may choose to transfer a sum of money to another player, who will either reciprocate or violate their trust. Over multiple rounds, participants typically learn whether to trust or distrust players based on their previous experience of social reciprocity (Anderhub, Engelmann, & Güth, 2002; King-Casas et al., 2005). On subsequent memory tests, healthy adults show enhanced face recognition and source memory for the associated behaviours of trustworthy and untrustworthy players encountered during the trust game (Bell, Buchner, & Musch, 2010), in keeping with evidence which suggests a distinct memory advantage for socially relevant information (Cassidy & Gutchess, 2014; Mitchell, Macrae, & Banaji, 2004; Rule, Slepian, & Ambady, 2012).

The current study sought to assess learning and memory of trust behaviour in AD and bvFTD patients using a trust game paradigm. We hypothesized that the use of social reciprocity as a form of feedback would improve learning over trials in AD patients but not bvFTD patients,

in line with the well-documented impairments in social and monetary reward processing in bvFTD (Melloni et al., 2016; Perry et al., 2015; Torralva, Roca, Gleichgerrcht, Bekinschtein, & Manes, 2009). Secondly, we aimed to explore whether memory for social interactions would be differentially enhanced in AD and bvFTD. We hypothesised that in bvFTD, the capacity for social enhancement of memory may be reduced, whereas the relative preservation of social cognition in patients with AD may facilitate their memory of social interactions. While no previous research has explored social memory enhancement in these patient groups, evidence of successful emotional memory enhancement in AD, but not bvFTD, supports this prediction (Kumfor, Irish, Hodges, & Piguet, 2013b; 2014). We anticipated that learning and memory of social interactions would correlate with atrophy in frontostriatal regions in bvFTD, reflecting the predominant social reward processing deficits in this patient group. In contrast, we expected that social learning and memory would correlate with the degeneration of predominantly MTL regions in AD, consistent with the primary deficit in memory mechanisms underpinning performance in this group. In addition, we aimed to examine the relationships between learning and memory for social interactions and day-to-day financial vulnerability in AD and bvFTD patients.

2. Materials and methods

2.1 Participants

Thirty-four dementia patients (bvFTD=20; AD=14) and 20 age-matched healthy controls were recruited through FRONTIER at Neuroscience Research Australia, Sydney. All bvFTD and AD patients fulfilled clinical diagnostic criteria for probable bvFTD (Rascovsky *et al.*, 2011) or probable AD (McKhann *et al.*, 2011), respectively. Disease duration was estimated as the number of years elapsed since the reported onset of symptoms. The Frontotemporal Dementia Rating Scale (FRS; Mioshi, Hsieh, Savage, Hornberger, & Hodges, 2010) and

Clinical Dementia Rating Scale (CDR; Morris, 1997) were used to determine disease severity in bvFTD and AD patients. All participants underwent general cognitive screening using the Addenbrooke's Cognitive Examination-III (ACE-III; Hsieh, Schubert, Hoon, Mioshi, & Hodges, 2013) to determine their overall level of cognitive functioning. Age-matched healthy controls were recruited from the FRONTIER research volunteer panel and scored >88 on the ACE-III (Hsieh *et al.*, 2013).

All participants provided written informed consent and this study was conducted in accordance with the Declaration of Helsinki. Ethical approval was obtained from the Human Research Ethics Committee of the South Eastern Sydney Local Health District and the University of New South Wales.

2.2 Background neuropsychology

All participants underwent a comprehensive neuropsychological assessment, including measures of attention (Castel, Balota, & McCabe, 2009; Castel, Balota, McCabe, & Castel, 2008), psychomotor speed (Trail Making Test (TMT), A time; Reitan & Wolfson, 1985), working memory (Digit Span Backward, total score; Wechsler, 1997) and cognitive flexibility (TMT, B – A time; Reitan & Wolfson, 1985). Verbal episodic memory (learning, recall and recognition) was assessed using the Rey Auditory Verbal Learning Test (RAVLT, sum of Trials 1–5, 30-minute recall score and corrected recognition (hits − false positives) score; Schmidt, 1996) and short-term visuospatial recall was assessed using the Rey Complex Figure Test (RCFT, 3-minute recall score; Rey, 1941).

2.3 Assessment of Social Vulnerability

The Social Vulnerability Scale (SVS; Pinsker, McFarland, & Stone, 2011) is a 15-item informant-rated questionnaire used to measure vulnerability to financial exploitation in older adults. The SVS comprises two subscales: credulity, the propensity to believe things that are unproven or unlikely to be true; and gullibility, the tendency to act upon these beliefs, usually in relation to outcomes of a financial nature. Each item is rated on a 5-point Likert scale, ranging from 0 (never) to 4 (always), with higher scores indicative of greater vulnerability. The SVS was completed by a relevant informant and was available for 16 bvFTD, 10 AD patients and 16 controls.

2.4 Trust game memory task

2.4.1 Stimuli and materials

To serve as trust game partners, images of 24 individuals (12 males, 12 females, age range 20–30 years) showing neutral facial expressions were selected from the Karolinska Directed Emotional Faces (KDEF) set (Lundqvist, Flykt, & Öhman, 1998). Twelve faces were randomly allocated as target stimuli, with four faces (two males, two females) in each learning condition (trustworthy, untrustworthy, lottery). The remaining 12 faces were presented as distractor stimuli during the face recognition memory test. Stimuli assigned per condition were counterbalanced across participants.

2.4.2 Practice phase

The trust game payoff structure and procedures for the learning and test phases are illustrated in Fig. 1. Following presentation of instructions, participants were shown examples of payoff outcomes for each possible response combination on the trust game (you ‘keep’, partner ‘shares’; you ‘keep’, partner ‘steals’; you ‘invest’, partner ‘shares’; you ‘invest’, partner

'steals'). Participants only proceeded to the learning phase of the experimental task if they could correctly indicate the amount of money they would receive in each payoff outcome.

FIGURE 1 AROUND HERE

2.4.3 Learning phase

We adapted a multi-round trust game (see for example, Fouragnan et al., 2013; van den Bos, van Dijk, & Crone, 2012), whereby participants always played the role of the investor and played multiple trust games with computerised partners. Social reciprocity strategies were kept consistent within each partner, such that trustworthy partners shared on 100% of trials and untrustworthy partners stole on 100% of trials (see Fig. 1A).

The following crucial manipulations were incorporated into our multi-round trust game:

1. Participants were told that their partners would make each 'share'/'steal' decision simultaneously. Both the participant's and partner's decisions were revealed, so that all participants received the same feedback about the trustworthiness of each partner, regardless of whether they chose to 'keep' or 'invest'. The trust game was self-paced but once a 'keep'/'invest' decision was made, outcome presentation was kept consistent across trials (6000 ms).
2. In order to contrast subsequent recognition memory for social versus non-social interactions, we adapted a lottery condition from Delgado, Frank and Phelps (2005). On these trials, there was a 50% probability of winning on each lottery round, and winnings were shared equally ($10 each; see Fig. 1A). The presentation and timing of lottery outcomes was consistent with trust game outcomes (6000 ms).

3. To limit working memory demands in patients, trials were divided into four blocks, with three different partners per block. Within each block, participants played six trust games with a trustworthy partner, six trust games with an untrustworthy partner and six lottery games with a lottery partner, in a randomised order (total trials = 72). The order of the blocks was counterbalanced across participants.

Participants were instructed to maximise their earnings throughout the learning phase but did not receive actual monetary payouts contingent on their performance, and they were not financially compensated for their involvement in the study. Feedback was provided at the end of each block regarding the total amount earned.

At the end of the learning phase, participants completed a brief affect rating task, to indicate how they felt following each of the 2 partner outcomes (share/steal) and 2 lottery outcomes (win/lose) on a 10 point Likert scale, ranging from 1 (very unhappy) to 10 (very happy). See Supplementary Materials.

To compare learning from social feedback across all trials in the trustworthy and untrustworthy conditions, the number of 'correct' responses in each condition was summed to yield a social learning accuracy score (i.e. 'invest' responses towards trustworthy partners and 'keep' responses towards untrustworthy partners; maximum score = 24). As responses and outcomes on lottery rounds were consistent across participants, these were not analysed.

2.4.4 Test phase

A surprise memory test was administered following a 20-minute delay, to assess face and source memory (Bell et al., 2010) (see Fig. 1B). Face recognition memory was assessed using

a two-alternative forced choice format with 12 trials. For faces correctly recognized, participants then made a source decision i.e., "What did this person do during the game?" ('share', 'steal', 'lottery' and 'don't know'). The 'don't know' response option was included to reduce potential contamination of guessing (Wong *et al.*, 2016). No feedback regarding response accuracy was provided throughout the task. Recognition trials were self-paced and presented in a random order.

For the test phase, outcome measures were percentage correct face recognition responses and percentage source memory responses, which were classified as 'source-recollected' (i.e. source-correct) or 'source-unrecollected' (i.e. 'source-incorrect' or 'source-don't know'). Given that source memory was only relevant following correct face recognition responses, trials were classified as 'source-unrecollected' when face recognition was incorrect. Source memory accuracy was calculated as the percentage of source-correct responses out of the total number of items in each condition (e.g. percentage source-correct $_{\text{trustworthy}}$ = (source-correct $_{\text{trustworthy}}$ / 4) × 100) (Rosa, Deason, Budson, & Gutchess, 2014).

2.5 Behavioural analyses

Data were analysed using SPSS 20.0 (SPSS Inc., Chicago, Ill., USA). Normally distributed variables, as determined by Shapiro-Wilks tests, were compared across groups using ANOVAs followed by Sidak post-hoc tests. Data that were not normally distributed were analysed using Kruskal-Wallis tests followed by *post hoc* pairwise comparisons, using Dunn's (1964) procedure, with Bonferroni correction for multiple comparisons. A chi-squared test was used to compare sex distribution across groups.

To contrast trust game memory task conditions across groups, measures of social learning accuracy, post learning phase affect ratings, face recognition accuracy and source memory accuracy were analysed using repeated measures ANOVAs. *Post hoc* simple-effects tests were conducted to examine differences between conditions within each participant group. All pairwise comparisons of the main effects and simple-effects were adjusted for multiple comparisons using the Sidak method.

Spearman rank correlations were used to examine relationships between learning (social learning accuracy) and memory of social interactions (source memory accuracy) and SVS variables. To contrast these associations across social (i.e. trustworthy and untrustworthy) and non-social (i.e. lottery) conditions, regardless of social reciprocity valence, we collapsed source memory accuracy for trustworthy and untrustworthy partners. A one-tailed significance level of $p<.05$ was applied for all correlational analyses.

2.6 Voxel-based morphometry analysis

Structural MRI brain scans were available for a subset of participants (18 bvFTD and 13 AD patients and 20 controls). Patients and controls underwent the same imaging protocol in accordance with previously reported standardised procedures (Irish, Piguet, Hodges, & Hornberger, 2014). A detailed description of image acquisition and pre-processing procedures is reported in Supplementary Material.

Voxel-wise general linear models (GLM) were applied to investigate differences in grey matter intensity via permutation-based non-parametric testing (Nichols & Holmes, 2002) with 5000 permutations per contrast. As a first step, group differences in grey matter intensity were tested for significance at $p <.005$, corrected for multiple comparisons via Family-Wise

Error (FWE) correction across space. A cluster extent threshold of 200 contiguous voxels was applied for group comparisons. Relative to controls, bvFTD and AD patients showed characteristic patterns of atrophy in keeping with their diagnoses (see Supplementary Table 1).

To identify the neural correlates of learning and memory of social interactions, correlations between learning and source memory scores in the social conditions and grey matter intensity were initially conducted across all participants combined. Next, to contrast the neural correlates of learning and memory of social interactions across patient groups, associations between grey matter intensity and social learning and source memory performance were investigated in each patient group separately. In accordance with previously reported procedures (Irish *et al.*, 2014; Sollberger *et al.*, 2009), patients and controls were included in the analyses to achieve greater variance in behavioural scores, thereby increasing the statistical power to detect brain-behaviour relationships. Finally, overlap analyses were conducted to identify common regions associated with social learning and source memory accuracy in bvFTD and AD. All trust game covariate analyses and overlap analyses were conducted at significance levels of $p<.001$, uncorrected for multiple comparisons, with a strict cluster extent threshold of 200 contiguous voxels. Regions of significant atrophy were superimposed on T1-weighted standard brain images, and regions of significant grey matter intensity decrease were localised with reference to the Harvard-Oxford probabilistic cortical atlas. Maximum coordinates for the anatomical locations of significant results are reported in MNI space.

3. Results

3.1 Demographics and background neuropsychology

Demographics and clinical characteristics of the participants are detailed in Table 1. Shapiro-Wilks tests indicated that age and functional impairment (FRS) data were normally distributed, whereas measures of disease duration and disease severity (CDR) showed non-normal distributions. Background neuropsychology variables showing a normal distribution included Digit span forwards and backwards, TMT A time and RAVLT learning total, with the remaining variables showing non-normal distributions.

Participant groups were matched for age (p=.085) and sex distribution (p=.155). An overall group difference was evident for total years of education (p=.029), with controls having completed more years of education than bvFTD patients (bvFTD vs. controls p=.024; AD vs. bvFTD p=.457). Importantly, the patient groups were matched for disease duration (p=.372) and disease severity (CDR, p=1.0). As expected, bvFTD patients were more functionally impaired relative to AD patients (FRS; p=.016).

On the ACE-III cognitive screening measure, both patient groups were significantly impaired relative to controls (both p values <.001), with comparable performance in the patient groups (p=.307). AD and bvFTD patients displayed characteristic cognitive profiles, with both patient groups showing deficits in attention (Digit span forwards; p values <.001), working memory (Digit span backwards; p values <.001) and cognitive flexibility (TMT B – A time; p values <.001) in relation to controls. AD patients showed poorer attention (Digit span forwards; p=.048) and psychomotor speed (TMT A time; p=.014) compared to bvFTD. Verbal episodic memory was significantly compromised in both patient groups relative to controls across measures of learning (RAVLT learning total; p values <.001) and recall (RAVLT 30-minute recall; p values <.001). Notably, learning performance (p <.001) was disproportionately disrupted in AD versus bvFTD, with a trend towards lower recall performance (p=.058). Verbal episodic memory recognition was comparably impaired in the

patient groups in relation to controls (RAVLT corrected recognition; bvFTD, AD vs. controls, *p* values <.001; bvFTD vs. AD, *p*=.318). Similarly, patients' nonverbal recall was significantly impaired relative to controls (RCFT recall, *p* values <0.001), with no significant differences between bvFTD and AD (*p*=.096).

TABLE 1 AROUND HERE

3.2 Social Vulnerability Scale

The subscale scores from the SVS are detailed in Table 1. Patients with bvFTD showed global difficulties on both credulity and gullibility subscales relative to controls (*p* <.001) and AD patients (credulity, *p*=.047; gullibility *p*=.038). While AD patients did not differ from controls on the gullibility subscale (*p*=.533), a trend towards higher credulity was present (*p*=.051), indicating a greater tendency to believe things that are unproven or unlikely to be true.

3.3 Trust game memory task results

3.3.1 Social learning

The total number of 'correct' responses, summed across learning trials according to condition is shown in Fig. 2. A significant main effect of group was evident ($F_{2,51}$=25.493, *p*<.001), indicating that learning accuracy was lower in AD (*p*<.001) and bvFTD (*p*<.001) patients compared to controls, but did not differ between patient groups (*p*=.996). A significant condition effect was also evident ($F_{1,51}$=6.531, *p*=.014), with learning accuracy higher in the untrustworthy compared to trustworthy condition, across all groups. No significant group × condition interaction ($F_{2,51}$=2.399, *p*=.098) was observed, though *post hoc* within group analyses suggested that within bvFTD patients, learning accuracy was higher in the

untrustworthy compared to trustworthy condition (p=.003), whereas learning accuracy did not differ across conditions within AD patients (p=.094) and controls (p=.846). Analyses of learning performance across each of the six learning trials for the trustworthy and untrustworthy conditions are detailed in Supplementary Material.

FIGURE 2 AROUND HERE

3.3.2 Neural correlates of social learning

Regions of grey matter intensity associated with social learning accuracy (sum of correct trust/distrust responses) in each patient group are shown in Table 2 and Fig. 4A. In bvFTD, social learning accuracy covaried with grey matter loss in the right orbitofrontal cortex and putamen, left temporoparietal junction (TPJ), and right frontal pole, and middle frontal, middle temporal and angular gyri and lateral occipital cortex. Social learning performance in AD was associated with grey matter intensity decrease in MTL regions including the amygdalae, hippocampi and parahippocampal gyri, bilaterally, as well as the left TPJ, right lateral occipital cortex and left cerebellum. The overlap analysis revealed that grey matter intensity decrease in the left TPJ covaried with social learning performance in both bvFTD and AD (Table 2).

TABLE 2 AROUND HERE

3.3.3 Memory for social interactions

Fig. 3A depicts face recognition accuracy for each condition across AD, bvFTD and controls. Analyses revealed a significant group × condition interaction ($F_{4,102}$=3.243, p=.015), with *post hoc* analyses indicating AD patients had significantly greater recognition of trustworthy

compared to lottery (p=.002) and untrustworthy (p=.001) faces. In contrast, no difference in recognition across conditions was seen in bvFTD patients (all p values >.741). Controls showed no significant difference in performance across conditions, likely due to their ceiling performance on this task (all p values >.986). The group effect for face recognition accuracy was significant ($F_{2,51}$=10.744, p<.001), with lower performance in AD patients than controls (p<.001) and a trend for lower performance in bvFTD patients relative to controls (p=.055), irrespective of condition. AD also tended to show lower face recognition accuracy than bvFTD (p=.057). A significant main effect of condition was also evident ($F_{2,102}$=4.311, p=.016), such that averaged across groups, face recognition accuracy was higher in the trustworthy compared to lottery condition (p=.027). Face recognition accuracy did not differ between the trustworthy and untrustworthy conditions (p=.121) or between the untrustworthy and lottery conditions (p=.598).

Fig. 3B depicts source memory accuracy for each condition across AD, bvFTD and controls (i.e. memory for the condition in which partners were encountered). Analyses revealed a significant group effect for source memory accuracy ($F_{2,51}$=35.886, p<.001), driven by lower accuracy in both bvFTD (p<.001) and AD (p<.001) patients compared to controls. Source memory accuracy was also lower in AD relative to bvFTD patients (p=.016). A significant main effect of condition was also observed ($F_{2,102}$=27.26, p<.001) with higher source memory accuracy in the trustworthy (p<.001) and untrustworthy (p<.001) conditions compared to the lottery condition. Surprisingly, the interaction between group and condition was not significant ($F_{4,102}$=.577, p=.68), with *post hoc* within group analyses confirming that all groups showed greater memory for social interactions (i.e. trustworthy and untrustworthy conditions), relative to non-social interactions (i.e. lottery condition) (all p values <.05).

FIGURE 3 AROUND HERE

3.3.4 Neural correlates of memory for social interactions

Regions of grey matter intensity associated with source memory accuracy for social interactions (trustworthy and untrustworthy) in each patient group are shown in Table 3 and Fig. 4B. In bvFTD, social source memory accuracy was associated with integrity of primarily frontostriatal regions (right orbitofrontal cortex, caudate, putamen, inferior and middle frontal gyri, left frontal pole, and paracingulate gyrus), as well as MTL regions (right amygdala, hippocampus, parahippocampal gyrus), bilateral temporoparietal regions extending to the insular cortex on the left, right posterior temporo-occipital regions (fusiform, inferior temporal and lateral occipital cortices), left fusiform cortex and right cerebellum. Regions of grey matter intensity covarying with social source memory performance in AD included bilateral MTL regions (amygdala, hippocampus, parahippocampal gyrus and temporal pole), as well as left TPJ, right temporo-occipital regions (inferior temporal, middle temporal cortices), and lateral occipital regions bilaterally. The overlap analysis indicated that grey matter intensity reduction in the left TPJ covaried with social source memory performance across both bvFTD and AD (Table 3).

TABLE 3 AROUND HERE

3.4 Relationships between trust game memory task performance and SVS variables

Finally, we examined whether learning and memory for social interactions (i.e. for trustworthy and untrustworthy partners) on the trust game was associated with susceptibility to financial mistreatment in AD and bvFTD (see Table 4). In AD patients, greater source memory accuracy in the social conditions correlated with lower credulity (r=–.677, *p*=.016)

and gullibility (r=–.603, *p*=.033) scores. No significant associations were identified between credulity, gullibility and source memory for non-social (lottery) interactions in AD (*p* values >.158). In contrast, credulity and gullibility scores did not correlate with source memory for social or non-social interactions in bvFTD (*p* values >.072). No significant associations were identified between learning and SVS subscale scores in either patient group (all *p* values >.136).

TABLE 4 AROUND HERE

4. Discussion

This is the first study to investigate learning and memory of social interactions using a novel neuroeconomic task across neurodegenerative disorders. Our results revealed a reduced capacity to learn socially relevant information on the trust game in both bvFTD and AD. Despite poor learning, however, a significant social enhancement effect for face and source memory was evident in AD. In contrast, face memory did not differ across social and non-social conditions in bvFTD. Unexpectedly, however, source memory was better for social interactions in bvFTD. Importantly, these behavioural findings were associated with financial vulnerability in the AD group only. Our neuroimaging analyses revealed divergent neural correlates of learning and memory of social interactions contingent on dementia subtype, with involvement of MTL and temporoparietal regions in AD, as opposed to a wider network of frontostriatal, insular, fusiform and MTL regions in bvFTD. The TPJ also emerged as a common neural substrate underpinning learning and memory of social interactions across both dementia syndromes, albeit with some differences in terms of laterality. Here, we discuss the implications of our findings in terms of the potential neurocognitive mechanisms

that underpin learning and memory of social interactions in these patient groups, as well as how the deficits uncovered here relate to susceptibility to financial exploitation in dementia.

4.1 Profile of performance in AD

Unlike healthy adults, AD patients did not appear to benefit from social reciprocity feedback during the learning phase of our trust game memory task. Poor learning of trust-related responses was associated with bilateral amygdala and hippocampal atrophy in AD, consistent with deficits in MTL-mediated memory encoding processes (Dickerson & Sperling, 2008; Rombouts et al., 2000), as well as the involvement of the amygdala in emotional memory in these patients (Mori et al., 1999).

Importantly, we found that social relevance significantly enhanced subsequent face memory in AD, despite marked episodic memory dysfunction. This social enhancement effect corroborates previous reports of preserved emotional memory enhancement in this patient group (Kalenzaga, Piolino, & Clarys, 2014; Kumfor et al., 2014; Kumfor, Irish, Hodges, & Piguet, 2013b). As memory for trust-related social interactions may incorporate emotional responses from such interactions, further studies are required to establish whether social and emotional aspects of experienced events may independently enhance memory. Moreover, the specificity of the social enhancement effect for trustworthy but not untrustworthy faces is an intriguing result, and adds to an increasing number of studies that demonstrate a positivity memory bias in AD (Sava, Krolak-Salmon, Delphin-Combe, Cloarec, & Chainay, 2016; Sava et al., 2015; Werheid, McDonald, Simmons-Stern, Ally, & Budson, 2011; Zhang, Ho, & Fung, 2015). As such, our findings highlight the importance of further research to investigate this positivity memory bias in face memory, especially given the potential therapeutic implications in supporting memory for social interactions in AD patients.

Source memory was also enhanced for social interactions in AD, though no positivity effect was observed. It is possible that trustworthy partners are more memorable at an implicit level, but when provided with cues regarding specific behaviours, memory for both trustworthy and untrustworthy partners is enhanced; a pattern which is consistent with that seen in healthy adults (Bell *et al.*, 2010). Our neuroimaging findings implicate similar amygdala-hippocampal regions across both learning and source memory performance. This corroborates the notion that learning and memory of trust-related social interactions in AD is associated with atrophy in brain regions that are crucial for not only retrieval, but also preferential encoding of emotionally-arousing stimuli (Klein-Koerkamp, Baciu, & Hot, 2012; Mori et al., 1999). While social enhancement of source memory in our study was evident following both positive and negative social reciprocity, further investigation is required to determine whether mechanisms that underlie social memory differ according to valence. Collectively, our behavioural and neuroimaging findings demonstrate that social relevance enhances memory of social interactions in AD.

4.2 Profile of performance in bvFTD

In bvFTD, poor learning of trust-related responses was associated with orbitofrontal and ventral striatal atrophy. Previous studies in healthy adults demonstrate that positive and negative social reciprocity on multi-round trust games engages orbitofrontal and ventral striatal regions (Phan, Sripada, Angstadt, & McCabe, 2010), which play a central role in reward-processing (O'Doherty, 2004). As such, our findings in bvFTD suggest that poor learning performance may be related to deficits in reward processing, in line with previous reports of reduced sensitivity to social and monetary gains and losses in this patient group (Perry *et al.*, 2015; Torralva *et al.*, 2009). Additionally, our imaging results in bvFTD point to

the broader involvement of occipital, lateral temporal-parietal-occipital and lateral prefrontal and frontopolar regions that are important for visual processing (Grill-Spector, Kourtzi, & Kanwisher, 2001), multi-sensory integration (Beauchamp, 2005) and executive aspects of learning and memory (Gilbert *et al.*, 2006; Long, Öztekin, & Badre, 2010), respectively. The mechanisms through which these regions may interact to support learning of socially relevant information warrants further investigation.

In terms of face memory, our results do not show evidence of a social enhancement effect in bvFTD, despite overall lower face memory in bvFTD than controls. Although it is possible that our recognition test format led to ceiling effects in bvFTD patients with milder memory impairment, bvFTD patients showed clear deficits relative to controls on background neuropsychological tests of episodic memory. Future investigations that employ more sensitive measures of face recognition memory may help clarify any enhancing effect of social relevance on face memory in this patient group.

Contrary to expectations, the source memory profile in bvFTD indicates that some aspects of memory are enhanced by social relevance, in contrast with previous reports of compromised emotional enhancement of memory in this group (Kumfor et al., 2014; Kumfor, Irish, Hodges, & Piguet, 2013b). Notably, however, the profile of behavioural performance was not correlated with everyday financial vulnerability. We speculate that while bvFTD patients may be able to remember social interactions, abnormal reward processing/motivation may lead to a failure to incorporate and modify decisions using this information. Our imaging results implicate a distributed network of social cognition, reward processing, memory, and both face and visual processing regions including the caudate, putamen and orbitofrontal cortex, together with the paracingulate cortex, insular cortex, frontal pole, amygdala,

hippocampus and fusiform and occipital cortices. The involvement of the paracingulate and insular cortices suggests that in addition to altered social reward processing, broader deficits in understanding social intentionality (Baez *et al.*, 2016; Walter *et al.*, 2004) and processing socio-emotional interoceptive cues (e.g. heart rate, skin conductance, muscle tension) (Craig, 2009; Sturm *et al.*, 2013) may also influence memory for socially relevant source details in bvFTD. Additionally, the involvement of the hippocampus suggests that source memory for social interactions may also be impacted by broader memory deficits in this patient group. Further research is necessary to understand these complicated relationships.

4.3. Shared neural correlates of social learning and memory performance in AD and bvFTD

It is interesting to note that the TPJ correlated with social learning and source memory performance, across both bvFTD and AD patients. The TPJ is a supramodal association area known to support a diverse array of cognitive functions, including Theory of Mind (Saxe & Kanwisher, 2003), reorienting of attention (Krall *et al.*, 2015), and attentional aspects of episodic memory retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). Notably, however, our results showed laterality effects across groups, such that the left TPJ was implicated in both AD and bvFTD, whereas the right TPJ was associated with source memory performance in bvFTD only. Although functional lateralisation of the TPJ is still debated, both hemispheres are commonly activated during social tasks in healthy adults (Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). Nonetheless, it has been proposed that the right TPJ plays a specific role in attributing mental states to others, whereas the left TPJ is more broadly involved in both mental and non-mental perspective taking (Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006; Samson, Apperly, Chiavarino, & Humphreys, 2004; Saxe & Wexler, 2005). Intriguingly, recent evidence has also implicated the right TPJ in

processing social motivations, in the context of altruistic behaviours (Morishima, Schunk, Bruhin, Ruff, & Fehr, 2012), social win/loss outcomes (van den Bos, Talwar, & McClure, 2013) or competition against familiar others (Sugimoto, Shigemune, & Tsukiura, 2016). Taken together, the specific involvement of right TPJ in bvFTD suggests that deficits in attributing intentions in socially-motivated contexts may also contribute to memory for social interactions. On the other hand, the shared involvement of left TPJ across groups likely relates to broader deficits in perspective taking, consistent with previous findings in both bvFTD and AD patients (Dermody *et al.*, 2016).

4.4 Implications for financial vulnerability

Identifying the extent to which memory for socially relevant information is associated with financial vulnerabilities is an important area to consider, given recent reports of financial abuse in patients with dementia (Lichtenberg, 2016; Tronetti, 2014). In AD, attenuation of the social memory enhancement effect was associated with higher susceptibility to the cognitive (credulity) and behavioural (gullibility) aspects of financial exploitation. The finding that these relationships were specific to AD concurs with the notion that general cognitive and memory deficits underlie financial errors in this syndrome (Chiong, Hsu, Wudka, Miller, & Rosen, 2013). These findings have clear implications for the awareness and management of such vulnerabilities. In particular, families and carers should bear in mind that social and emotional significance may continue to support memory retrieval in AD patients, particularly during the earlier stages of the disease. Indeed, emotional experiences in AD appear to persist beyond the ability to recall specifics of the event which caused the emotion, thus reinforcing the importance of fostering positive emotional experiences in these patients (Guzmán-Vélez, Feinstein, & Tranel, 2014). With disease progression, however, and

worsening of memory impairment and emotion recognition abilities (Bertoux, de Souza, et al., 2015b), AD patients may be increasingly susceptible to social and financial mistreatment, and require further support in navigating day-to-day social and financial interactions.

In contrast, despite the fact that susceptibility to financial exploitation was disproportionately higher in bvFTD patients, this was unrelated to learning and memory of social interactions. This lack of association suggests a mediating factor between social memory and credulity/gullibility exists. As such, memory for social interactions in bvFTD does not seem to play a central role in their susceptibility to financial mistreatment. Instead, our neuroimaging findings support the notion that these susceptibilities may be related to deficits in socio-emotional functions and reward processing (Chiong et al., 2013; Perry & Kramer, 2013). Interestingly, bvFTD patients did not rate their experiences of the trust game differently to controls or AD patients, suggesting a disconnect between affective reactions and the ability to modify behaviour accordingly. The veracity of these affective ratings should be interpreted with caution, however, given that bvFTD patients may fail to integrate socio-emotional interoceptive information in order to recognise their own emotions (Sturm, Ascher, Miller, & Levenson, 2008). Future research that incorporates formal measures of socio-emotional functioning and reward processing is necessary to explore these associations.

Together, these findings suggest that while bvFTD patients appear to learn and remember aspects of socially relevant information, they do not apply this knowledge to modulate their behaviour. Of interest, failure to modify behaviour within specific social contexts has been proposed to underlie impaired social cognition in bvFTD (Ibanez & Manes, 2012). As such, examining the influence of contextual details, such as reputation for trustworthiness (Fouragnan *et al.*, 2013) or moral character (Delgado *et al.*, 2005), represents an important

area of future enquiry, especially considering recent evidence of impaired integration of social contextual information during normative decision-making (O'Callaghan *et al.*, 2016) and social bargaining (Melloni *et al.*, 2016) in bvFTD.

A number of methodological limitations warrant further discussion. Firstly, the nature of the participants' responses on the learning phase of the trust game (i.e. to 'keep' or 'invest') did not allow us to distinguish between learning about the partner's *trustworthiness* and learning how best to *respond* to the partner's trustworthiness, as the learning performance scores only reflect the latter. Given that feedback regarding the partner's trustworthiness was kept constant regardless of each participant's response, it is possible that some patients were able to learn about the partner's *trustworthiness* but lacked the cognitive capacity to *deploy this information*. Importantly, this may explain why both AD and bvFTD patients showed a social memory enhancement effect despite poor learning performance on the trust game. To address this limitation, future studies should directly contrast passive viewing versus interactive paradigms. In addition, given the potential dissociation between subjective ratings versus objective physiological measures of affective responses (Sturm *et al.*, 2008), future investigations of social learning using the trust game paradigm may benefit from simultaneously recording psychophysiological responses. Finally, we used a two-alternative forced choice face memory recognition test to minimize patient fatigue and reduce the likelihood of floor effects. While this allowed us to detect a significant social enhancement effect on face memory in AD, ceiling effects were evident in controls. Our face memory results should therefore be interpreted with this caveat in mind. Furthermore, the neural correlates of socially relevant face recognition in these patient groups should be explored in future studies that employ more sensitive measures of face recognition memory.

In summary, this study is the first to investigate learning and memory of social interactions in AD and bvFTD, using a neuroeconomic trust game paradigm. While patients with AD may harness socially relevant information to facilitate memory retrieval, learning and memory of social interactions is strongly associated with the degeneration of episodic memory and emotion processing structures in the MTL, and is therefore vulnerable to decay with increasing disease severity. Most strikingly, this effect is associated with susceptibility to financial exploitation in AD, raising important ethical implications for the care of individuals living with dementia. Conversely, the memory advantage for socially relevant information does not appear to mitigate the striking financial vulnerabilities reported in bvFTD. Instead, such vulnerabilities are likely exacerbated by widespread social cognitive deficits and altered reward processing. From a broader theoretical perspective, our findings provide important insights regarding the complex interplay between social cognition and memory, and the devastating effect caused by a breakdown in these processes.

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Table 1. Demographic and clinical characteristics of the study cohort[a]

	Control	bvFTD	AD	Group effect		Post hoc test
				Statistic	*p*	
Sex (M:F)	8:12	14:6	7:7	$\chi^2 = 3.724$	.155	
Age (years)	63.29 (6.53)	62.23 (8.03)	68.06 (8.52)	*F(2,53)* = 2.590	.085	
Education (years)	13.18 (1.99)	11.14 (2.19)	12.23 (2.93)	*F(2,53)* = 3.815	.029	Con > bvFTD
Disease duration (years)	-	5.96 (3.16)	5.58 (4.37)	*H(2)*= .797	.372	
CDR SoB [18]	0.10 (0.21)	5.82 (3.17)	4.73 (2.07)	*F(2,49)* = 37.448	<.001	Con < bvFTD, AD
FRS Rasch score	-	–0.84 (1.45)	0.50 (1.53)	*t(1,32* = 6.434	.016	bvFTD < AD
ACE-III [100]	95.75 (3.45)	75.60 (11.90)	64.29 (11.61)	*H(2)* = 39.714	<.001	Con < bvFTD, AD
Digit span forward [16]	12.20 (2.02)	9.10 (2.36)	7.36 (1.34)	*F(2,53)* = 25.788	<.001	Con > bvFTD > AD
Digit span backward [14]	8.35 (1.90)	5.15 (1.81)	4.21 (2.15)	*F(2,53)* = 22.520	<.001	Con > bvFTD, AD
TMT A time (seconds)	30.42 (7.34)	46.50 (17.36)	127.64 (153.04)	*F(2,53)* = 6.755	.003	Con, bvFTD < AD
TMT B – A time (seconds)	35.89 (14.18)	106.35 (63.32)	249.70 (147.29)	*H(2)* = 29.189	<.001	Con < bvFTD, AD
RAVLT learning total [75]	54.25 (7.93)	36.69 (8.62)	21.36 7.53)	*F(2,53)* = 70.088	<.001	Con > bvFTD > AD
RAVLT 30-min recall [15]	10.65 (3.10)	5.19 (2.93)	1.93 (1.59)	*H(2)* = 34.230	<.001	Con > bvFTD, AD
RAVLT corrected recognition (hits – false positives) [15]	12.55 (2.48)	2.88 (6.34)	–3.14 (6.79)	*H(2)* =31.206	<.001	Con > bvFTD, AD
RCFT 3-min recall [36]	19.83 (5.10)	8.63 (6.65)	2.77 (3.50)	*H(2)* =31.884	<.001	Con > bvFTD, AD
SVS credulity [28]	3.88 (3.16)	13.00 (5.44)	8.40 (5.19)	*F(2,41)*= 15.535	<.001	Con, AD < bvFTD
SVS gullibility [32]	1.50 (1.46)	9.25 (7.52)	3.80 (4.83)	*F(2,41)*=8.929	.001	Con, AD < bvFTD

[a] Standard deviations in parentheses, maximum score for tests shown in brackets.

Clinical Dementia Rating Scale (CDR); Frontotemporal Dementia Rating Scale (FRS); Addenbrooke's Cognitive Examination (ACE-III); Trail Making Test (TMT); Rey Auditory Verbal Learning Test (RAVLT); Rey Complex Figure Test (RCFT); Social Vulnerability Scale (SVS).

Table 2. Voxel-based morphometry results showing regions of grey matter intensity decrease that covary with social learning in bvFTD and AD.

Regions	Hemisphere (L/R/B)	MNI Coordinates			Number of voxels	*t-score (peak voxel)*
		X	Y	Z		
bvFTD						

Lateral occipital cortex (superior)	R	24	-78	16	1213	4.89
Superior temporal gyrus (posterior), planum temporale, parietal operculum cortex	L	-54	-38	10	505	4.89
Middle temporal gyrus (temporo-occipital), angular gyrus, lateral occipital cortex (inferior)	R	50	-52	-4	442	4.89
Frontal pole	R	6	68	-6	289	4.89
Orbitofrontal cortex, putamen	R	36	20	-18	281	4.89
Middle frontal gyrus	R	34	28	26	229	4.89
AD						
Superior temporal gyrus (anterior), central opercular cortex, parietal operculum cortex, supramarginal gyrus (posterior), angular gyrus, insular cortex, Heschl's gyrus, planum temporale	L	-60	-2	0	1369	4.99
Cerebellum	L	-38	-44	-36	1066	4.99
Parahippocampal gyrus (anterior), hippocampus, amygdala	R	26	-2	-30	692	4.99
Hippocampus, amygdala, parahippocampal gyrus (anterior)	L	-20	-14	-24	406	4.99
Lateral occipital cortex (superior)	R	30	-86	24	301	4.99
Overlap						
Planum temporale, parietal operculum cortex	L	-48	-34	14	240	4.71

Results uncorrected at $p < .001$ and at a cluster extent threshold of > 200 contiguous voxels.
L = left; R = right; B = bilateral; MNI = Montreal Neurological Institute.

Table 3. Voxel-based morphometry results showing regions of grey matter intensity decrease that covary with source memory of social interactions in bvFTD and AD.

Regions	**Hemisphere (L/R/B)**	**MNI Coordinates**			**Number of voxels**	***t-score (peak voxel)***
		X	**Y**	**Z**		
bvFTD						

Orbitofrontal cortex, caudate, putamen, amygdala, hippocampus, parahippocampal gyrus	R	8	12	-24	1713	4.89
Cerebellum, fusiform cortex (posterior), inferior temporal gyrus (temporo-occipital), lateral occipital cortex (inferior)	R	56	-62	-38	1166	4.89
Frontal pole, paracingulate gyrus	L	-24	60	-10	596	4.89
Insular cortex, central opercular cortex, parietal operculum cortex, planum temporale	L	-32	-20	14	587	4.89
Inferior frontal gyrus, middle frontal gyrus	R	40	14	26	300	4.89
Planum temporale, central opercular cortex	R	58	-18	4	292	4.89
Fusiform cortex (anterior and posterior)	L	-36	-14	-44	220	4.89
AD						
Planum temporale, parietal operculum cortex, central opercular cortex	L	-48	-28	8	662	4.99
Parahippocampal gyrus (anterior), temporal pole, amygdala, hippocampus	R	28	-6	-34	650	4.99
Inferior temporal gyrus (temporo-occipital), middle temporal gyrus (temporo-occipital), lateral occipital cortex (inferior)	R	50	-44	-16	531	4.99
Amygdala, hippocampus, temporal pole	L	-28	0	-26	490	4.99
Lateral occipital cortex (superior), occipital pole	R	24	-88	22	419	4.99
Lateral occipital cortex (superior)	L	-12	-76	42	286	4.99
Lateral occipital cortex (superior)	L	-38	-70	10	270	4.99
Lingual gyrus	L	-20	-56	0	245	4.99
Occipital pole	L	-18	-98	-16	232	4.99
Overlap						
Parietal operculum cortex, central operculum cortex, planum temporale	L	-46	-34	16	248	4.71

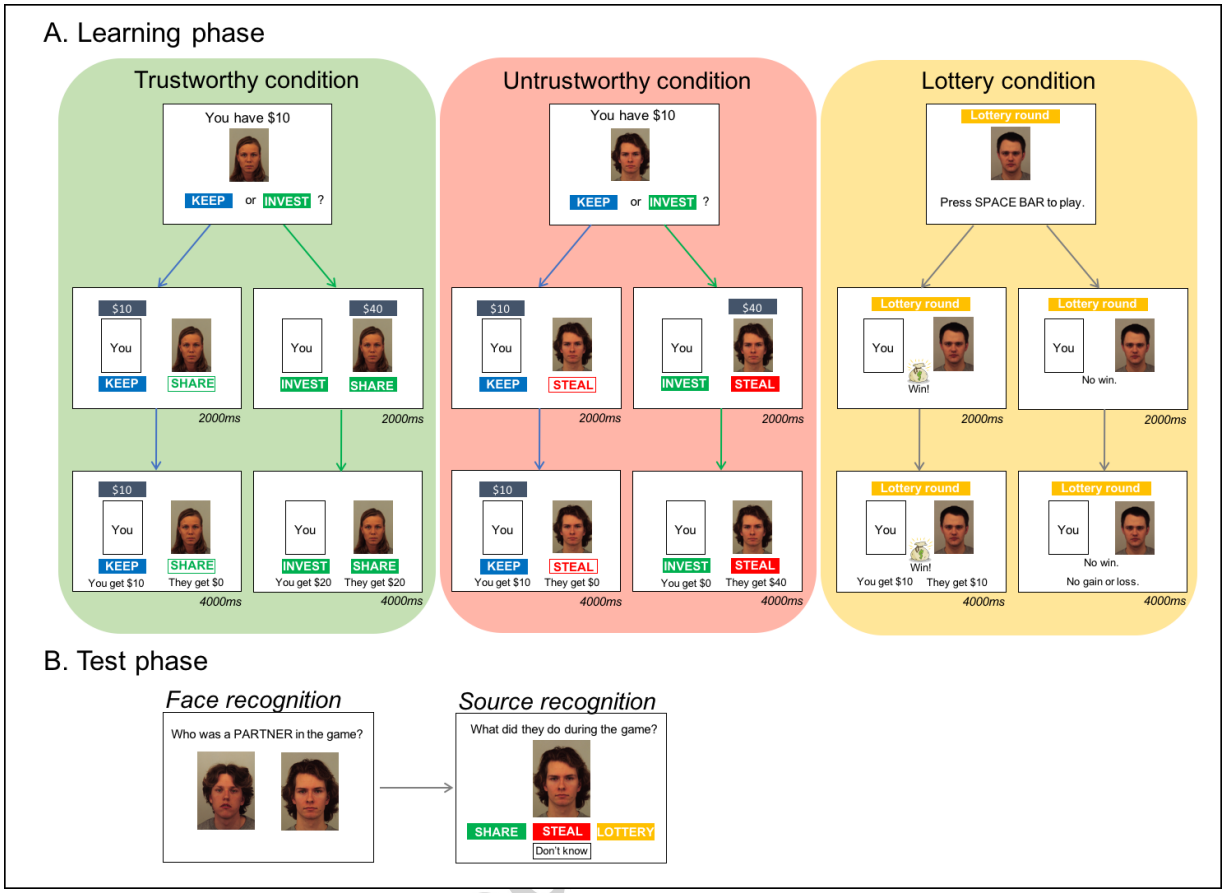
Results uncorrected at $p < .001$ and at a cluster extent threshold of > 200 contiguous voxels.
L = left; R = right; B = bilateral; MNI = Montreal Neurological Institute.

Table 4. Spearman rank correlation coefficients from analyses exploring associations between SVS variables, social learning and source memory accuracy for social and non-social partners from the trust game.

		Social Vulnerability Scale	
		Credulity	**Gullibility**
bvFTD	**Social learning**	-0.231	0.292
	Source memory		
	Social	-0.108	0.467
	Non-social	0.002	0.352
AD	**Social learning**	-0.219	-0.379
	Source memory		
	Social	**-0.677***	**-0.603***
	Non-social	-0.317	-0.353

Correlation coefficients representing significant one-tailed correlations are shown in bold typeface (*p<.05). Higher scores on the Social Vulnerability Scale (SVS) denote greater impairment.

Fig. 1. (A) Example of trials and possible outcomes across trustworthy, untrustworthy and lottery conditions in the learning phase of the trust game memory task. (B) Example of face and source memory questions in the test phase of the trust game memory task.



Each round of the trust game began with a screen displaying the image of a partner with the written instructions 'You have $10. Keep or invest?'. If the participant decided to 'keep' (i.e. distrust), they retained the $10 in their account and the partner received $0, regardless of whether they chose to 'share' or 'steal'. If the participant decided to 'invest' (i.e. trust), their $10 was transferred to the partner's account and quadrupled in value ($40). Then, if the partner chose to 'share' (i.e. reciprocate trust), the $40 was divided evenly, resulting in $20 for each player. Alternatively, if the partner chose to 'steal' (i.e. violate trust), they retained the $40 in their account and the participant received $0. Participants did not make any trust-related responses on the lottery game.

Fig. 2. Social learning accuracy (total 'invest' responses for trustworthy partners and total 'keep' responses for untrustworthy partners) in the trustworthy and untrustworthy conditions across groups. Error bars represent standard error of the mean

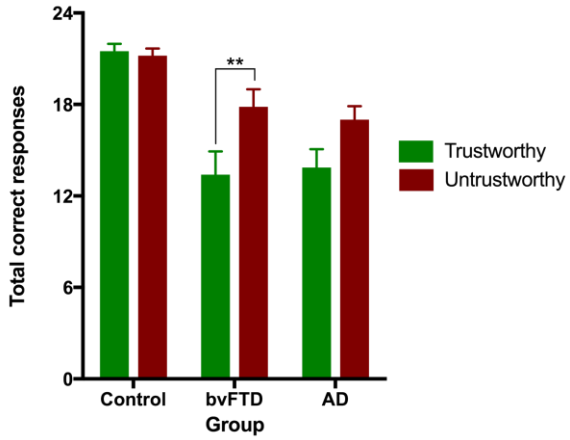


*Fig. 3. (A) Percentage face recognition accuracy across conditions and groups on the two-alternative forced-choice recognition test. (B) Percentage source memory accuracy for each condition across groups. Error bars represent standard error of the mean. Brackets indicate significant post hoc simple effects, *p<.05, **p<.01, ***p<.001.*

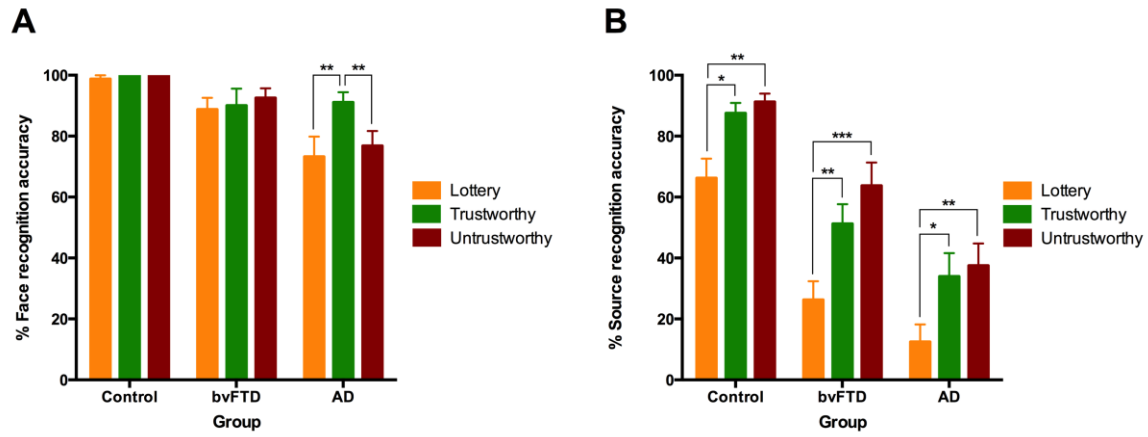


Fig. 4. Voxel-based morphometry (VBM) results showing areas of significant grey matter intensity decrease correlating with (A) Social learning on the trust game; (B) Source memory of social interactions. Neural correlates for bvFTD and AD patients shown in red and blue, respectively. Results uncorrected at p<.001 and at a cluster threshold of >200 contiguous voxels.