Higher or lower? The functional anatomy of perceived allocentric social hierarchies.

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[*]Professor Sean Spence died on 25th December 2010 aged 48. We dedicate this paper to his memory.

Shortened Title: fMRI of social hierarchies.

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Abstract

The perception and judgement of social hierarchies forms an integral part of social cognition. Hierarchical judgements can be either self-referential or allocentric (pertaining to two or more external agents). In psychiatric conditions such as dissocial personality disorder and schizophrenia, the impact of hierarchies may be problematic. We sought to elucidate the brain regions involved in judging allocentric social hierarchies. Twenty-two healthy male subjects underwent three fMRI scans. During scanning, subjects answered questions concerning visually-presented target pairs of human individual's relative superiority within a specific social hierarchy or their perceived degree of social alliance (i.e., whether they were "friends or enemies"). Subjects also made judgements relating to target pairs' age, gender and fame to control for confounding factors and performed a baseline numerical task. Response times increased in line with hypothesized ascending executive load. Both social hierarchy and social alliance judgements activated left ventrolateral prefrontal cortex (VLPFC), left dorsal inferior frontal gyrus (IFG) and bilateral fusiform gyri. In addition, social alliance judgements activated right dorsal IFG and medial prefrontal cortex. When compared directly with social alliance, social hierarchy judgements activated left orbitofrontal cortex. Detecting the presence of social hierarchies and judging other's relative standing within them implicates the cognitive executive, in particular the VLPFC. Our finding informs accounts of 'normal' social cognition but our method also provides a means of probing the dissocial brain in personality disorder and schizophrenia where executive function may be dysfunctional.

Keywords: functional magnetic resonance imaging (fMRI); social hierarchy; social alliance; ventrolateral prefrontal cortex; orbitofrontal cortex; dissocial personality.

1.0 Introduction

Despite a recent tendency, particularly in the West, to under-emphasize the stratified nature of society, hierarchies persist within the work place, families and among larger social groups. Indeed, human social hierarchies cohere rapidly and may be observed in children as young as two years of age (Boyce, 2004). Hierarchical structures provide an order of superiority and responsibility, while also offering a system within which individuals may identify goals, expectations and self-worth. Furthermore, an understanding of hierarchical superiority facilitates civilised and appropriate behaviour, from parental authority to due legal process. In Victorian Britain, the Social-Darwinist philosopher Herbert Spencer went as far as to argue that social hierarchies were essential to preventing societal disintegration. Spencer (1820-1903) believed that hierarchies on a societal-level enabled effective governance and on an individual level underpinned a sense of self-control (Spencer, 1896, p.109).

However, social hierarchies are dynamic by nature. Movements up and down the social ladder are often perceived as being closely associated with notions of success and failure, which are themselves closely aligned with concepts of dominance and submission (Price et al., 1967; O'Connor et al., 2007, pp. 49-76). Furthermore, those at higher levels within a stable hierarchical system often enjoy better psychological well-being and better physical health (Bosma et al., 1998; Adler et al. 2000; Cohen, 2004, Chiao. 2010), though this effect is actually reversed in unstable hierarchies, where high-ranking individuals experience more stress due to continuous attacks on their position (Zink et al., 2008; Setchell et al., 2010). The nature of the advantage in stable hierarchies may not be purely a matter of relative position, however, rather the *magnitude* of the disparity between the higher and lower social levels may be key.

Evidence suggests that countries with greater inequality between rich and poor have populations with lower overall health and well-being than countries where the disparity is less marked (Wilkinson, 1996).

The perception and interpretation of social hierarchies may be self-referential, relating to a person's own perceived position within them, but can also be allocentric, concerning the hierarchical relationship pertaining between two or more external agents. It is these latter judgements of external hierarchies that form the basis for the current study.

The way that an individual judges such allocentric hierarchical relationships may partially depend on intrinsic personality factors such as the degree to which their own behaviour is balanced between 'approaching' in response to rewards and non-punishments (the Behavioural Activation System [BAS]; Gray, 1994, pp. 243-247) and 'withdrawing' from non-rewards, punishments and novelty (the Behavioural Inhibition System [BIS]; Gray, 1982). In one study (Demaree et al., 2005), those individuals with a higher BAS strength were more likely to relate to the dominant character in a presented dyad, which was shown to induce a positive affect, whilst those with a higher BIS sensitivity were more inclined to relate to the submissive character, inducing a negative affect. This raises the intriguing possibility that our personalities and our subjective comprehension of social hierarchies may interact to impact our social success and sense of well-being. Hence, if this is even partially true, elucidating the biological bases for the perception and interpretation of social hierarchies would be important for our understanding of psychological well-being and

perhaps certain psychiatric disorders, particularly when the person may perceive themselves at the bottom of the social ladder.

Evidence for a biological basis to the recognition of one's own and others' positions in a social hierarchy includes neuropharmacological research in animals (Yeh et al., 1997; Tierney and Mangiamele, 2001; Raleigh et al., 1991), gene-environment models of social hierarchy across species (Chiao. 2010) and brain development, lesional and functional neuroimaging research in humans (e.g., Raizada and Kishiyama, 2010). Relevant to the neuropharmacology of social hierarchy, there is a well-established link between serotonin and reward (e.g. Schweighofer et al., 2008) and, in keeping with this, a number of studies have reported that the social hierarchical consequences of successful performance are of comparable salience to monetary reward (Izuma et al., 2008; Zink et al., 2008).

Previous neuroimaging studies of social hierarchy, though few in number, have adopted a range of perspectives. In separate event-related potential (ERP) and fMRI studies, Chiao and colleagues (2008) examined temporally- and spatially-distinct neural responses to two kinds of facial cues, emotional expressions and facial postures, and how they contributed to social dominance perception. Specifically, aggression-related emotional expressions (e.g. fear) resulted in increased ERP activation sensitivity (early latency [~120ms] and higher amplitude), whilst dominant and submissive facial posture processing occurred relatively later (~200ms). Equally, spatially, there were distinct fMRI activations associated with fear and anger expressions (in fronto-limbic regions) and dominant and submissive facial postures (in right superior temporal, lingual and fusiform gyri). In a further neuroimaging

study by Chiao and colleagues (2009a), judgements on the social status hierarchy of cars, uniform insignias and faces of naval officers were studied in a group of Midshipmen undergoing Naval Reserve Officer Training (such subjects become expert at recognising social status from these visual symbols). A baseline comparator test of numerical magnitude was also undertaken. Both social status hierarchy and numerical comparisons recruited distinct and overlapping regions of bilateral intra-parietal sulcus (IPS). Furthermore, the degree of activation within IPS corresponded with semantic distance in both social status and number tasks. Finally, in a third neuroimaging study, Chiao and colleagues (2009b) examined the phenomenon of 'social dominance orientation' or whether individual humans intrinsically prefer a social dominance hierarchy across groups or a more egalitarian philosophy (challenging the notion that hierarchical societies are humans' default mode of organisation). In an empathy (other's pain perception) paradigm conducted in fourteen healthy female subjects, anterior insula and anterior cingulate cortex activation predicted an individual's stated preference for a social dominance hierarchy. Specifically, subjects expressing a preference for a social dominance hierarchy showed reduced fronto-insular activation when perceiving another's pain. These results were interpreted as evidence of "a neural foundation for social and political attitudes underlying prosocial behaviour" and also the proposition that human social hierarchies may have a fundamental biological basis.

Other neuroimaging studies with a peripheral relevance to social hierarchies have investigated decision-making (Rogers et al., 2004; Sakagami, 2006), personal social interaction (Schilbach et al., 2006; Adolphs, 2003) and deception (Spence et al., 2004, 2008). In the latter case, Spence and colleagues (2008) described a region of left

VLPFC that was activated not only during vocal deception (lying) but also by 'compliance' with the demands of an investigator: a novel finding that raised the intriguing possibility that 'inauthentic' responding, within a social milieu, might implicate left VLPFC. This finding has resonance with the proposal by Adenzato and Ardito (1999, pp. 7-12) that deceptive responding and social hierarchies may be somewhat mutually reinforcing, in that the ability to produce the former facilitates a primate's survival in the latter.

Psychiatrically, difficulties in understanding and respecting hierarchies and authority figures are prevalent in some personality disorders (Blair, 2003, 2007, pp. 3-17). In Conduct Disorder, Dissocial Personality Disorder and Psychopathic Personality Disorder the diagnostic criteria allude to impaired judgments concerning authority and appropriate behaviours within a hierarchical context (DSM-IV, APA, 1994).

In summary, the perception and interpretation of social hierarchies seems to be a key part of our social cognitive apparatus and has a demonstrable impact upon our physical and psychological health. However, little work has been undertaken to identify those brain regions involved in this form of higher cognitive processing, particularly the recognition and judgment of allocentric social hierarchies.

We hypothesized that the perception and interpretation of social hierarchies would be a high level executive function and would therefore engage (activate) prefrontal cortices. Moreover, we hypothesized that explicit judgements about social hierarchies would activate VLPFC / orbitofrontal cortices (Blair, 2004). Finally, we hypothesized that response times would be related to the level of executive function involved in

social hierarchical or sub-component judgements and therefore that the resulting higher cognitive load would lead to longer response times. Due to possible gender-specific differences in social status perception and experience (Hess et al., 2000; Mehta et al., 2008), we opted to study only male subjects.

2.0 Methods

2.1 Stimulus development

The behavioural paradigm consisted of showing healthy subjects computerized images of two people at a time and was designed to elicit choices referring to the relative positions of these people within their social hierarchies. However, we also wished to examine those factors that might reasonably be predicted to confound such hierarchical judgments, specifically: older age, male gender and relative fame (Figure 1). Furthermore, by way of a 'higher-level' control task, we considered what we termed the two target individuals' social alliance, by enquiring as to whether they were "friends or enemies?" This was possible, using images of people who were famous and whose interactions might thereby be surmised by our volunteer observers. Finally, two 'lower-level' baseline number-judgement conditions were designed for comparison with the active conditions, comprising judging which of two numbers was higher or lower or whether a pair of numbers was equal (see Figure 1). These two baseline conditions were designed so that the form of the proposed questions and answers matched those of the more complex active conditions (i.e. "which number is higher / lower?" matching with social hierarchy, gender, age and fame questions and eliciting a response of 'higher' or 'lower'; and "are the numbers equal?" matching with social alliance questions and eliciting a response of 'yes' or 'no' [see Figure 1]). We used images of 63 different people which were administered in varied pairs across

the experiment (i.e. the same image appeared in different pairs relating to different judgements). Pre-scanning piloting confirmed that all the famous people shown were easily recognised by the planned target demographic (male undergraduate students) and that the correct answer was unambiguous for all the age, gender and fame pairings.

INSERT FIGURE 1 ABOUT HERE PLEASE

2.2 Subjects and demographic profile.

Twenty-four healthy male, right-handed (Edinburgh Handedness Inventory; Oldfield, 1971) subjects were originally recruited to the study, though two subjects' imaging data were subsequently excluded due to excessive head movement during scanning. Hence, data from twenty-two subjects (mean age = 24.2 years; mean years of education = 16.9) were analysed. Subjects had an estimated mean IQ of 120 (National Adult Reading Test [NART]; Nelson, 1982). No subjects reported a history of psychiatric or neurological disorder. Written informed consent was obtained following full explanation of the protocol, which had been approved by the University of Sheffield Research Ethics Committee.

2.3 fMRI imaging

Subjects underwent three eight-minute functional magnetic resonance imaging (fMRI) scans at 3.0 Tesla (Achieva, Philips Medical Systems, Best, NL) at the University of Sheffield. Each scan comprised 160 time points - single shot echo planar imaging (EPI); repeat time (TR) = 3000ms; echo time (TE) = 35ms; field of view (FOV) = 230mm; matrix size = 128 x 128; 32 x 4mm thick slices. Subjects also underwent a

single, high-resolution structural scan (3D gradient echo, MP-RAGE, TR = 10.5ms; TE = 4.8ms; resolution = 0.8mm^3).

2.4 Imaging paradigm

In a counterbalanced, alternating A-B boxcar design, subjects viewed either five pairs of human faces or five pairs of numbers via an MR compatible, radiofrequency-head coil integrated computer screen (Eloquence, InVivo Corp, Orlando, FL, USA). During each condition, subjects made a forced choice between, for example, which of two faces was 'lower' in their social hierarchy or which of two numbers was 'higher'. Each stimulus pair was presented for 5 seconds and subjects responded with their right index or middle finger using an MR-compatible button-box. All stimuli pairings were repeated across runs with the opposite question asked (e.g. "who is higher in their social hierarchy?" and "which number is lower?"; c.f. above). Stimuli choices and response times were recorded.

2.5 Data analyses

Response time data were analysed using the general linear model (repeated measures ANOVA) with *post-hoc* pair-wise comparisons in SPSS version 14.0. Scan data were analysed in Statistical Parametric Mapping (SPM2) (www.fil.ion.ucl.ac.uk/spm) within Matlab version 7.1 (The MathWorks, Inc., MA, USA). Images were pre-processed by correcting for movement, normalized to a standard EPI template (voxels: 2mm^3) and smoothed using a Gaussian kernel of 10mm, full-width half-maximum. A 128sec cut-off high pass filter was applied at the first level of analysis (no AR1 correction for serial correlations was applied as we planned to use a second level mixed-effects analysis). Stimuli judgement blocks were entered for each subject

at the first level and modelled by a canonical haemodynamic response function and its temporal derivative. First-level, weighted, fixed-effects analyses were conducted on individual scans examining two contrasts of interest:

i)   Social hierarchy judgement epochs minus fame, age, gender and 'number higher / lower' judgement epochs.

ii)   Social alliance judgement epochs minus 'number equal' judgement epochs.

A second level, random-effects, analysis was performed using the resulting contrast images from each subject's first level fixed-effect analysis, which theoretically allows inferences to be drawn concerning the population as a whole from which the subjects were recruited. All analyses were conducted at $p<0.05$ corrected for family-wise error (FWE) and are reported with an extent threshold of 30 voxels.

3.0 Results

3.1 Behavioural

Judgements posited *a priori* as requiring increasing executive brain resources were associated with significantly increasing response times ($F_{6,38}=160$; $p<0.001$; Figure 2). *Post-hoc* pair-wise comparisons were all highly significant ($p<0.001$) except for a trend level significant difference between the 'number equal' and gender conditions ($p=0.052$). The percentage of incorrect responses was less than 5% (mean = 3.4%; SD = 0.9%) for all conditions except social alliance (16%) where the judgements were necessarily more subjective.

INSERT FIGURE 2 ABOUT HERE PLEASE

3.2 Functional anatomical

Activations associated with social alliance judgements contrasted with 'number equal' judgements included left ventrolateral prefrontal cortex (VLPFC; Brodmann Area [BA] 47), bilateral dorsal inferior frontal gyrus (IFG; BA 45 / 46), medial prefrontal cortex (mPFC; BA 8 / 9 / 10), anterior cingulate cortex (ACC; BA 6 / 32) and bilateral fusiform gyri (BA 19 / 37). There was also extensive posterior cortical activation, including cuneus / lingual gyrus (BA 17 / 18) and cerebellum (Table 1a; Figure 3).

INSERT TABLE 1 AND FIGURE 3 ABOUT HERE PLEASE

Activations associated with social hierarchy judgements contrasted with fame, age, gender and 'number higher / lower' judgements included left VLPFC (BA 47), left dorso-posterior IFG (BA 44/45) and bilateral fusiform gyrus (BA 18 /19). Again, there was extensive posterior cortical activation, including cuneus / lingual gyrus (BA 17 / 18), left inferior occipital gyrus (BA 18) and cerebellum (Table 1b; Figure 4).

INSERT FIGURE 4 ABOUT HERE PLEASE

Difference maps between social hierarchy and social alliance judgements (i.e. comparison of the above contrasts) showed social hierarchy to be associated with greater activation of left orbitofrontal cortex (OFC; BA 11; peak z = 4.87; [Talairach and Tournoux (T&T), 1988] co-ordinates: -42, 42, -12; Figure 5). There was also a large amount of posterior-ventral activation, including bilateral parahippocampal gyri and cerebellum. The reverse contrast (social alliance greater than social hierarchy)

showed no significant difference at a p<0.05 FWE corrected threshold. However, at a more liberal threshold (p<0.001, uncorrected for multiple comparisons) there was greater activation of right medial prefrontal cortex (BA 9; peak z = 3.30; co-ordinates: 12, 48, 22) and bilateral precuneus / intra-parietal sulci (BA 7 / 40; peak z = 4.02; co-ordinates: 26, -42, 52 and; peak z = 3.79; co-ordinates: -22 -46 43).

INSERT FIGURE 5 ABOUT HERE PLEASE

4.0 Discussion

We set out to examine the neural correlates of allocentric judgements made concerning the relative social (hierarchical) status pertaining between pairs of third-party individuals: in other words, the brain processes implicated in judging 'who is higher' or 'who is lower' in the social context. In order to isolate the specific neural processes concerned, we also controlled for the neural correlates of a number of likely confounding variables, which might be expected to impact the allocation of hierarchical status (e.g., male gender and older age). In addition, by way of a 'high-level' comparator, we examined the neural correlates of judgements concerning the likely social alliances of such perceived pairings (i.e., whether they were likely to be 'friends or enemies'). While our hierarchical judgements required accurate recognition of social status, the alliance judgements required something else, an awareness of social interactions attributed to those actors in the past (e.g., whether they were publicly known to be on good or bad terms). Hence, the judgement of social alliances was a demanding high-level comparator, which required some background knowledge of the perceived dyad (e.g., Tony Blair and Gordon Brown). As expected, we found that the response times exhibited by subjects increased in magnitude in line

with hypothesized magnitude of cognitive load. In particular, our two 'high-level' conditions incurred the greatest processing time penalties. This suggests that they are indeed (cognitively) hierarchically superior to the other conditions we examined. In addition, we found that both 'higher' processes implicated the prefrontal executive, which was again in keeping with our review of the pre-existing literature (above). We found that judgements concerning the social hierarchical and social alliance relationships pertaining between pairs of third-party human agents were both associated with activations of left VLPFC and left dorsal IFG, suggesting that the left prefrontal cortex is implicated in both these socially targeted processes. The role of VLPFC in modulating and judging socially appropriate behaviour has been previously ascertained from lesional studies including the well-known case of Phineas Gage. Gage famously suffered severe damage to either left (Ratiu et al., 2004) or bilateral (Damasio et al., 1994) prefrontal cortices in an accident sustained whilst working on a railway (a 'tamping iron' passed through his skull). Despite retaining "full possession of his reason", Gage was subsequently described by his foreman as, "... manifesting but little deference for his fellows…" (amid other personality changes implicating impulse-control; Harlow, 1868). Similarly, the 'therapeutic' prefrontal leucotomies conducted in the early twentieth century, whilst apparently successful at treating severe psychoses, by creating a post-operative euphoria and carefree patient, came at a cost. Patients were observed to become less respectful of social normality as well as exhibiting impairments of concentration, initiative, spontaneity, and abstract reasoning (Dolan, 2007). More recent studies of patients with discrete prefrontal cortical lesions have also shown impaired behavioural responses to certain hierarchies (Karafin et al., 2004), a deficit in social perception (Mah et al., 2004), defective social decision-making (Eslinger and Damasio, 1985; Barrash et al., 2000) and impaired

social reasoning in response to authority and punishment (Anderson et al., 1999).

Contrary to part of our hypothesis we have not reported OFC activation in response to

the main social hierarchy versus relevant contrasts condition; only when directly

comparing between social hierarchy and social alliance conditions. One plausible

explanation for this observed pattern of activation is a relative OFC decrease during

the social alliance judgment condition, though this was not apparent on the reverse

contrast. Technically, OFC consists of BAs 10, 11 and 47 (Kringelbach, 2005), which

would in fact make our left IFG activations describable as OFC. Specifically, the

activations we reported for social alliance and social hierarchy individually (T&T co-

ordinates -42 30 -13 and -44 30 -13 respectively) are directly caudal to those reported

for the social hierarchy versus social alliance comparison (T&T co-ordinates -42 42 -

12). This highlights the large overlap between regiono-functional descriptions such as

left OFC and neuroanatomical descriptions such as left IFG. However, to

acknowledge that these (all technically) OFC activations are in different BAs we

chose to describe the posterior BA 47 foci as left IFG. Both the social hierarchy and

social alliance conditions were also associated with activation of bilateral fusiform

gyri and widespread posterior cortical regions including lingual gyrus. The latter

finding suggests that a broader network of brain regions, both 'higher' and 'lower',

rostral and caudal, is activated in concert when more complex processing is required

(e.g., judging hierarchical status elicits more from the network than a more superficial

judgment, such as 'who is older?').

Compared with social alliance judgements, social hierarchy judgements were

specifically associated with increased activation of left OFC, in a region lying anterior

to VLPFC. This again seems to emphasize the importance of the *left* prefrontal

executive in salient social hierarchical judgements (implicating left VLPFC, OFC and dorsal IFG, above). It suggests that over and above the processing that is required to accurately identify dyadic pairs, and their perceived social relationship (in terms of friendship or enmity) there is something specific to the question of hierarchical status that engages the left orbitofrontal cortex (below). In the reverse contrast (albeit only significant at a lower statistical threshold), we found social alliance judgements to be associated with increased activation of right mPFC and bilateral intra-parietal sulcus. Social alliance judgements were also associated with activation of mPFC and ACC and right dorsal IFG.

What are the neural processes 'supporting' a hierarchical judgement? To begin with, VLPFC, recently shown to have a role in implicit dominance perception from body posture (Marsh et al., 2009), is known to facilitate control of attention towards the task in hand (Wolf et al., 2006), inhibits pre-potent responses (Spence et al., 2008) and resists distraction by 'temptations', thereby allowing a measured deliberation over problems. These precursors to behavioural modulation, often act in concert with the OFC (which assigns reward values to specific stimuli; Rolls, 2000; Bunge and Zelazo, 2006), and may be particularly engaged where context is important, i.e., when the 'correct' behaviour depends upon where you find yourself in the hierarchy. The OFC also has a role in 'reactive aggression' or the exhibition of 'appropriate' aggression (in primates) depending on contextual hierarchical relationships, which may pathologically be disturbed as dissocial personality disorder in humans (Blair, 2004; Spence, 2009, pp.340-347). Furthermore, the VLPFC's role in the inhibition of pre-potent responses also makes it central to lying (Spence et al., 2008) and 'inauthenticity'. Deception may be an essential attribute for surviving in a hierarchical

environment as otherwise an organism might have no freedom of manoeuvre (Adenzato and Ardito, 1999, pp. 7-12). The flexibility of social hierarchies, across time and context, requires constant updating of rules governing social behaviour (retrieved via the OFC) and self-monitoring of its impact (Beer et al., 2006). Retaining in mind and following such conditional rules again involves the VLPFC, but also the DLPFC. Both regions have been reported to be sensitive to rule complexity (Crone et al., 2006) and are thus more active when assessing stimuli that elicit different responses depending on a rule appropriate to the current context (bivalent stimuli) than when they assess stimuli associated with invariant responses (univalent stimuli). The application of such rules to regulate both behaviour and emotions may range from entirely automatic to explicitly willed (Mauss et al., 2007). Within the prefrontal cortex an anterior-posterior, rostral-caudal, distinction has also been reported, with more complex or abstract reinforcers (such as monetary gain and loss) being represented more rostrally in the OFC than less-complex reinforcers such as taste (Kringelbach, 2005). Finally, awareness of social blunders, as measured by the 'faux pas' test, is compromised in patients with OFC dysfunction, who cannot judge when something socially awkward has happened despite appearing to understand a story perfectly well (Stone et al., 1998). Hence, in summary, multiple cognitive processes which might be hypothesized to contribute to the executively demanding process of establishing allocentric social hierarchies have been localised to VLPFC and OFC interactions and these areas' modulating influences.

Turning to posterior brain regions, the role of fusiform gyrus and lingual gyrus in self-referential dominance perception has been reported before (Chiao et al., 2008). Chiao and colleagues measured event-related potentials (ERPs) and used fMRI to examine

responses to perceived submission and dominance communicated by facial expression and posture. Activations were obtained relative to neutral faces using regression analyses from post-scanning behavioural ratings. It is notable that this subconscious social dominance / hierarchy perception paradigm elicited some similarities with our explicit forced-choice paradigm, but did not show the frontal-executive activations seen in our results. In their further study (Chiao et al., 2009b) a link between social dominance orientation (an individual's preference for a more hierarchical or egalitarian society) and empathy was made. Using a 'painful versus neutral scenario' paradigm this study (which used only female participants) reported anterior cingulate cortex activation to be correlated with social dominance orientation, independent of their dispositional empathy scores. However, the overlapping concepts of social cognition, empathy and theory of mind (which have also been associated with the fusiform and lingual gyri; Adolphs, 2001; Völlm et al., 2006) and their contributions to, or underpinning of, social hierarchy judgements has yet to be fully elucidated. Finally, in a study of the neuro-conceptual link between egocentric social and physical space (Yamakawa et al., 2009), bilateral parietal cortices were implicated. This 'social distance' condition also activated bilateral visual cortices, fusiform gyri, medial frontal cortex and inferior frontal cortices (as well as insula, basal ganglia and amygdala). Our bilateral intra-parietal sulcus result for the social alliance condition contrasted with the social hierarchy condition is therefore in keeping with Chiao and colleagues findings associating this region with comparison of numerical and social status magnitude (Chiao et al., 2008) and Yamakawa and colleagues 'social distance' study (Yamakawa et al., 2009).

We had no specific *a priori* hypotheses regarding the main-effect reverse contrasts (number equal greater than social alliance; number higher / lower, fame, age and gender greater than social hierarchy). However, p*ost hoc* examination of these reverse contrasts showed significant activation of inferior parietal lobule (BA 40) – right lateralised for number higher / lower; bilateral, together with posterior cingulate cortex, for number equal. These findings (though *post*-hoc, and thus subject to suitable caution) are consistent with the reported role of inferior parietal lobule in mathematical reasoning (as opposed to calculation; Kroger *et al*. 2008). We also had no specific *a priori* hypotheses about the influence of reaction time (RT) on our neuroimaging results, but given the significant differences in RT between conditions, a *post-hoc* simple regression analysis was conducted. Individuals' mean response times for active conditions were entered as regressors with first-level contrast images. No significant correlational relationship between neural response and reaction time was revealed in our data.

5.0 Limitations

A possible confound in the social hierarchy versus baselines contrast is that social hierarchy judgments require the retrieval of declarative memory content for both individuals, whereas age and gender can be inferred based on the pictorial content, while fame requires the identification of one individual, but not the other. However, as the same pictorial stimuli were used repeatedly (e.g. a "who is older?" question may have related to two famous individuals) it would seem likely that episodic / semantic memory retrieval was frequently invoked, whether strictly required or not. Hence this confound will likely have been minimised by the automatic, though often unnecessary memory retrieval processes associated with all judgement conditions. As

we studied only male subjects we are unable to comment as to whether our findings are gender-specific, though research in social dominance orientation (e.g. Caricati., 2007) would suggest that differences are likely to exist. Relatedly, we did not have sufficient statistical power to investigate whether the gender of dyadic subjects in the judgement tasks was relevant. Furthermore, it is possible that participants additionally (implicitly) assessed their own (self-referential) social hierarchical status in relation to the task subjects, particularly with respect to social-dominance perception (Chiao et al., 2008). Finally, in common with much fMRI research we have on occasion utilised 'reverse inference', referring to previous studies' cognitive function localisations to interpret brain activations rather than specifically investigating these functions. Using such reverse inferences has been previously criticised for the potentially limited information provided, particularly when the selectivity of the region in question cannot be established (Poldrack. 2006). Future social hierarchy research would undoubtedly benefit from the inclusion of paradigm conditions which manipulate these proposed constituent psychological variables.

6.0 Conclusions

Our fMRI study of allocentric social hierarchical and social alliance judgements has shown robust left VLPFC, OFC, bilateral dorsal IFG and fusiform gyrus activations which are associated with high level executive functions and social dominance perception. Given the difficulties of recognising and respecting social hierarchies in certain psychiatric disorders, further investigation of the neural substrates of such judgements in patient populations may be informative of disordered social cognition and its neural bases.

7.0 Acknowledgements

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Figure Legends

Figure 1. Examples of picture stimuli pairs and questions asked. N.B. During the actual scanner task, only pictures (and not individual's names) were shown.

Figure 2. Mean response times (ms ± 1SD) for all categories of stimuli pairs, showing increasing response time associated with increased executive processing load. All conditions are significantly different from each other (($F_{6,38}$=160; p<0.001; repeated measures ANOVA) except 'number equal' and 'gender', which exhibit a trend difference (p=0.052; *post-hoc* pair-wise comparisons).

Figure 3. SPM brain maps of activations associated with social alliance ('friend or enemy') judgements contrasted with 'number equal' judgements. 22 subjects; p<0.05 corrected for family-wise erroe (FWE); extent threshold = 30. Contrast estimates (index units with 90% confidence intervals) are shown below for all relevant clusters (see Table 1a).

Figure 4. SPM brain maps of activations associated with social hierarchy judgements contrasted with fame, age, gender and 'number higher / lower' judgements. 22 subjects; p<0.05 corrected for family-wise erroe (FWE); extent threshold = 30. Contrast estimates (index units with 90% confidence intervals) are shown below for all relevant clusters (see Table 1b).

Figure 5. SPM brain maps showing greater activations associated with social hierarchy judgements compared with social alliance ('friend or enemy') judgements.

22 subjects; p<0.05 corrected for family-wise erroe (FWE); extent threshold = 30. The

contrast estimate (index units with 90% confidence intervals) is shown below for the

left orbitofrontal cortex cluster.

Figure 1. Examples of picture stimuli pairs and questions asked.

HRH Prince Harry   HRH Queen Elizabeth II

"Who is higher/ lower in their social hierarchy?"

Charlotte Church   HRH Prince Philip, Duke of Edinburgh

"Who is older / younger?"
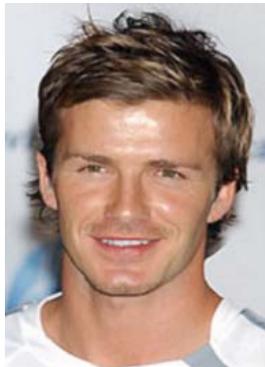
David Beckham   Catherine Zeta-Jones

"Who is male / female?"

Unknown waitress   Tony Blair

"Who is more / less famous?"

7   1

"Which is higher / lower?" or *"Are the numbers equal?"*


Angelina Jolie

Jennifer Aniston

"Are they friends?" or *"Are they enemies?"*

**Figure 2.**
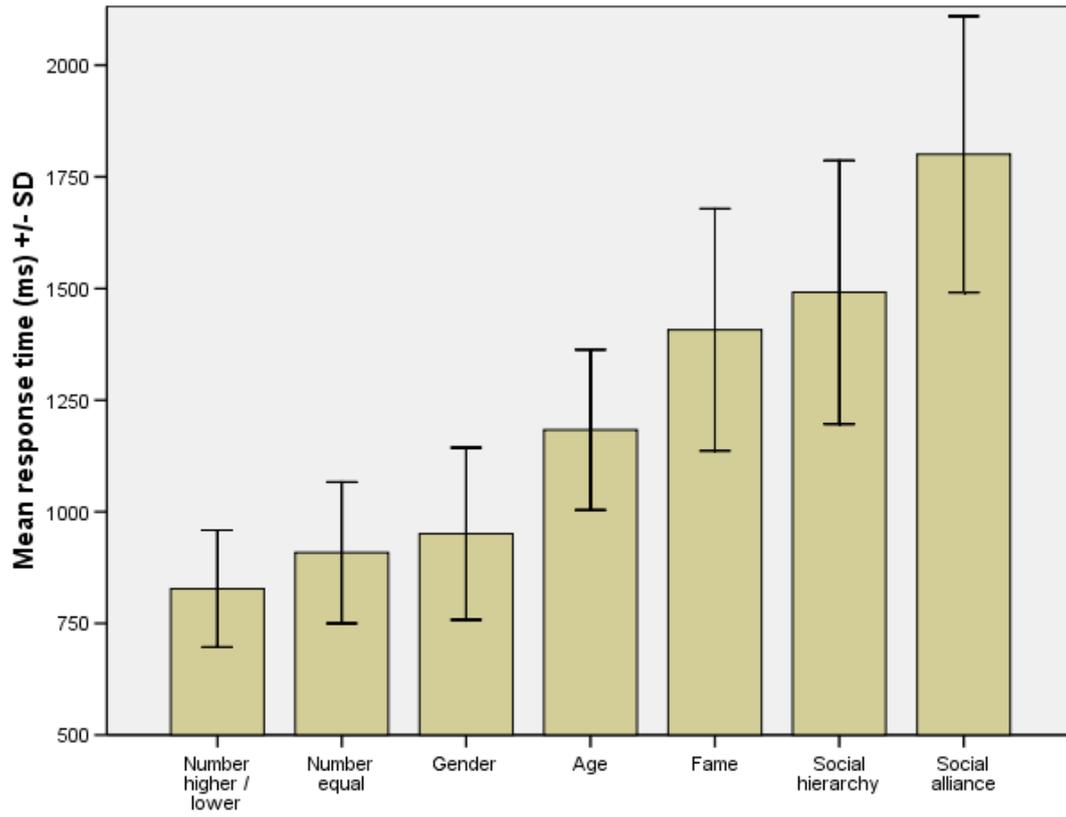
Figure 3.
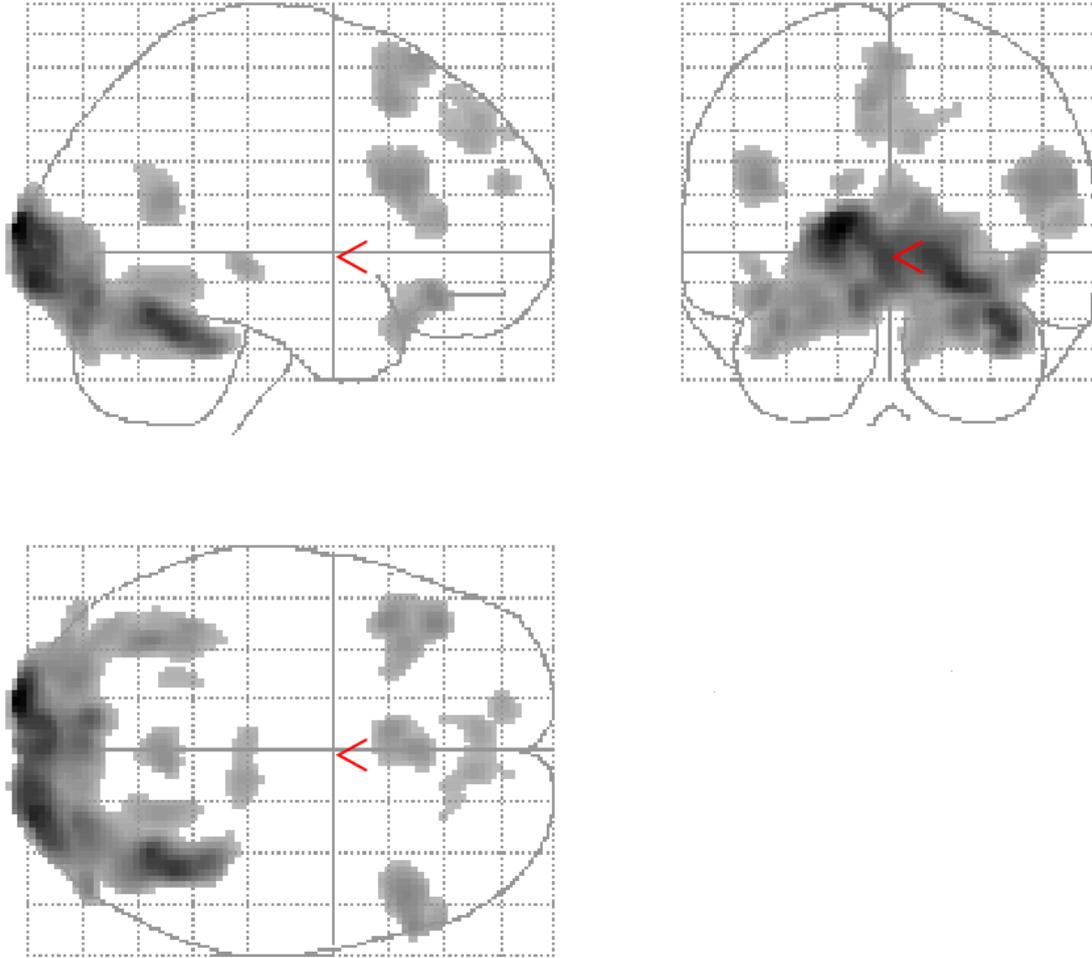
Figure 4.
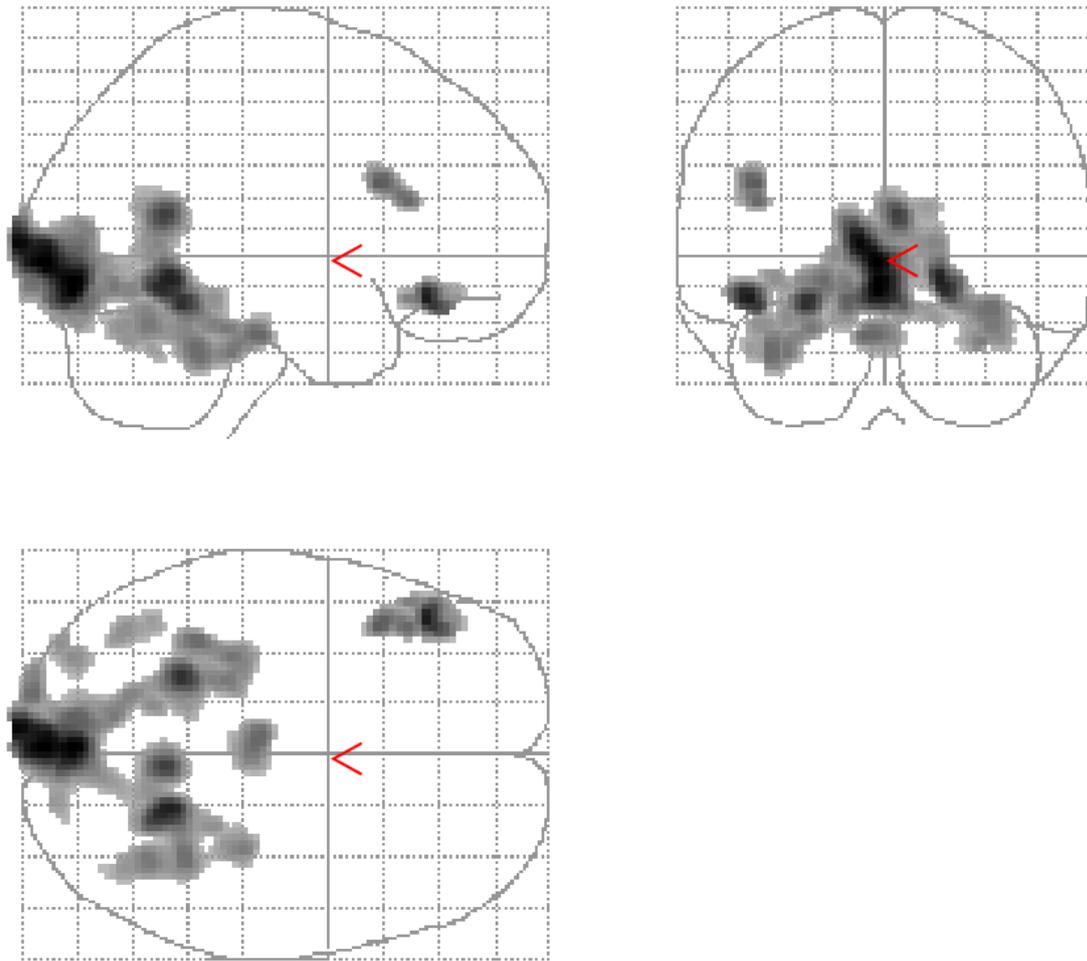
Figure 5.
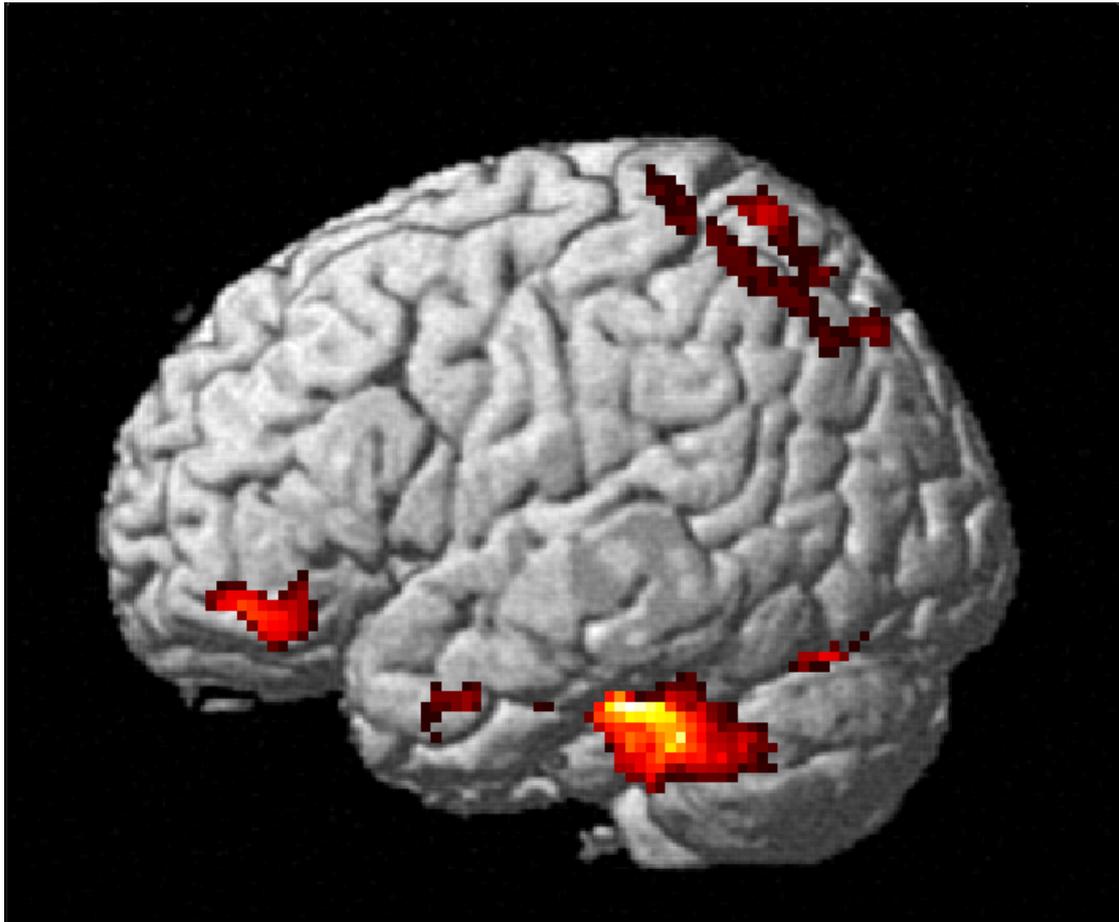
Table 1a. Social alliance *vs.* 'number equal' (see figure 3).

Anatomical region	BA	X	y	z	Z-value	Extent
Rt. inferior frontal gyrus	45/46	48	24	21	6.80	594
		57	*26*	*21*	*6.73*	
		57	*33*	*9*	*6.36*	
Lt. inferior frontal gyrus	45	-42	18	21	6.77	258
	47	-42	30	-13	6.78	414
		-34	*22*	*-20*	*6.54*	
Medial prefrontal cortex	8/9	8	46	33	6.30	335
		-6	*48*	*36*	*6.29*	
		4	*49*	*40*	*6.08*	
	9/10	-14	55	17	6.25	43
	8/6	0	30	56	6.62	405
		2	*20*	*56*	*6.33*	
Anterior cingulate cortex	*6/32*	*-6*	*20*	*45*	*6.57*	
Lt. Cuneus	18	-16	-100	12	Inf	8265
Rt. lingual gyrus		*22*	*-95*	*-4*	*Inf*	
Rt. fusiform g. / cerebellum	*37*	*40*	*-51*	*-19*	*7.75*	
Lt. fusiform g. / cerebellum	19/37	-24	-49	-9	5.95	44
Rt. post. cingulate gyrus	23/31	4	-51	19	6.60	235
Rt. parahippocampal gyrus	30	10	-29	-2	6.37	107
Periaqueductal grey-matter		*-2*	*-27*	*-2*	*6.16*	

Table 1b. Social hierarchy *vs.* fame, age, gender & 'no. higher / lower' (see figure 4).

Anatomical region	BA	x	y	z	Z-value	Extent
Lt. inferior frontal gyrus	47	-44	30	-13	7.09	165
		-49	*25*	*-13*	*6.29*	
	44/45	-42	17	21	6.59	139
		-42	*26*	*15*	*6.48*	
Lt. fusiform gyrus	18/19	-32	-82	-13	6.15	111
Lt. inferior occipital gyrus		*-36*	*-86*	*-2*	*6.13*	
Rt. fusiform gyrus	19	18	-51	-4	6.22	135
Lingual gyrus / cuneus	17/18	-2	-82	-3	7.31	4591
		-2	*-89*	*3*	*7.30*	
		-8	*-99*	*9*	*7.21*	
Lt. Cerebellum		-40	-67	-17	6.13	130
		-44	*-57*	*-22*	*5.97*	
Brainstem		-6	-22	-21	6.51	194

Co-ordinates are shown in standardized neuroanatomical space (Talairach and Tournoux, 1988). BA = Brodmann's area. Lt. = left. Rt. = right. post. = posterior. g. = gyrus. Inf.= infinity. Co-ordinates in *italics* refer to sub-clusters of the preceding activation.