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Understanding the influence of personality on dynamic social gesture processing: An fMRI study



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ABSTRACT

This fMRI study aimed at investigating how differences in personality traits affect the processing of dynamic and natural gestures containing social versus nonsocial intent. We predicted that while processing gestures with social intent extraversion would be associated with increased activity within the reticulothalamic–cortical arousal system (RTCS), while neuroticism would be associated with increased activity in emotion processing circuits. The obtained findings partly support our hypotheses. We found a positive correlation between bilateral thalamic activity and extraversion scores while participants viewed social (versus nonsocial) gestures. For neuroticism, the data revealed a more complex activation pattern. Activity in the bilateral frontal operculum and anterior insula, extending into bilateral putamen and right amygdala, was moderated as a function of actor-orientation (i.e., first versus third-person engagement) and face-visibility (actor faces visible versus blurred). Our findings point to the existence of factors other than emotional valence that can influence social gesture processing in particular, and social cognitive affective processing in general, as a function of personality.

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1. Introduction

Personality refers to an integrated pattern of thinking, feeling and behaving that varies among individuals, but remains stable within each individual across time (Suslow et al., 2010). It is often measured by applying the Five-Factor Model (FFM) comprised of five higher order factors that encompass observed behavioral variation (Costa and McCrae, 1992; Grimm et al., 2012; Suslow et al., 2010). Amongst these factors, extraversion and neuroticism are the most widely studied in cognitive and affective neuroscience (Canli et al., 2002; Hutcherson et al., 2008; Kehoe et al., 2012; Mobbs et al., 2005; Servaas et al., 2013; Suslow et al., 2010). Although a large number of studies have explored the role of personality in neural processing of emotional stimuli, very few have examined how personality affects neural processing of natural social interactions.

1.1. Behavioral characteristics of extraversion and neuroticism

Behaviorally, the introversion/extraversion dimension captures the social aspects of personality. While extraversion is

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characterized by a propensity to be assertive, to experience excitement and positive affect and to enjoy social interactions (Hutcherson et al., 2008; Lucas et al., 2000), introversion is characterized by a tendency to avoid social situations and to be reserved or socially awkward (Wright et al., 2006). Individuals with higher extraversion scores are differentially sensitive to reward cues in the environment. This enhanced reward sensitivity is considered to be the source of higher sociability in extraverts (Lucas et al., 2000). Neuroticism, on the other hand, captures differences in personality traits associated with negative emotions (e.g., anxiety, fear, worry, envy and jealousy). Although a personality dimension, neuroticism carries high clinical relevance as it is considered a risk factor for developing anxiety and depressive disorders (Kendler et al., 2004). Behaviorally, individuals with high neuroticism scores are characterized as having persistent sensitivity to negative cues in the environment (Wright et al., 2006). Further, individuals with higher neuroticism scores assess social situations as more threatening as compared to individuals with lower neuroticism scores (Schneider, 2004).

1.2. Anatomical neuroimaging data for extraversion and neuroticism

Several neuroimaging studies have attempted to link variation in neural circuits (both anatomical and functional) with individual differences in personality. Examining such relationships may allow us to develop more nuanced understanding of how differences in



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neural circuits underlie individual differences in personality and behavior.

A large number of studies have examined the neuroanatomical basis of individual differences in personality using volume based morphometric (VBM) analysis. In so doing, extraversion has been shown to be *positively* related to regional volume of the medial orbitofrontal cortex (DeYoung et al., 2010; Grodin and White, 2015), nucleus accumbens (Grodin and White, 2015), left temporal cortex, dorsolateral prefrontal cortex (DLPFC), anterior cingulate (Grodin and White, 2015; Kapogiannis et al., 2013), and left amygdala (Omura et al., 2005); and negatively related to regional volume of the bilateral amygdala and parahippocampal (Lu et al., 2014), right middle temporal gyrus, inferior frontal gyrus (Bjørnebekk et al., 2013; Wright et al., 2006) and right temporoparietal junction (Forsman et al., 2012). On the other hand, also using VBM analysis, neuroticism has been positively associated with volume of right cerebellum (Lu et al., 2014), middle temporal gyrus and cingulate cortex (DeYoung et al., 2010; Omura et al., 2005); and *negatively* correlated with right orbitofrontal cortex, DLPFC, amygdala and precentral gyrus (DeYoung et al., 2010).

Taken together, these VBM-based studies lack convergence in results and the observed variability in findings has been recently attributed to the use of inconsistent nuisance covariates across studies (Hu et al., 2011).

1.3. Functional neuroimaging data for extraversion and neuroticism

Using functional Magnetic Resonance Imaging (fMRI), researchers have also examined how individual differences in personality affect dynamical processing of a given stimulus. A large proportion of these studies examined effects of personality on processing emotional stimuli in general. For example, Park et al. (2013) examined how extraversion and neuroticism are related to differences in brain reactivity to musical stimuli expressing happiness, sadness and fear. Neuroticism was observed to be positively associated with activations in basal ganglia, insula and orbitofrontal cortex in response to happy music (Park et al., 2013). No significant findings were observed for extraversion. In another study, Kehoe et al. showed participants positive or neutral images from the International Affective Picture System (IAPS; (Lang et al., 2008)), and asked participants to subjectively rate these images on arousal and valence. Parametric fMRI analysis was also used to examine the relationship between stimulus-modulated brain activity and personality. High levels of neuroticism were observed to be associated with attenuated reward processing (i.e., reduced activation in the orbitofrontal cortex), and a complex pattern of activation was observed with high levels of extraversion during arousal processing within the reticulothalamic-cortical arousal system (RTCS) (Kehoe et al., 2012). Furthermore, Hutcherson and colleagues designed a clever study to dissociate the effects of attention from that of personality on neural processing of emotion. They used evocative film clips as stimuli and instructed participants either to passively observe the films or to attend to and continuously rate their emotions while watching the films (Hutcherson et al., 2008). Using this design, they were able to suggest that attentional focus did not influence the relation between personality and neural response to positive emotional stimuli (Hutcherson et al., 2008).

Finally, other studies have also examined the role of personality during neural processing of emotional speech cues (Brück et al., 2011) and anticipation of emotional images (Brühl et al., 2011).

Although the aforementioned findings represent an important basis for our understanding of how personality could influence emotion processing in general, very little is known about how personality may affect neural processing of social (versus nonsocial) content. Processing social information is particularly salient to human behavior (Hariri et al., 2002; Vrtička et al., 2012). Thus, examining how personality affects neural computations associated with processing social stimuli, in healthy individuals, provides a unique opportunity for deriving hypotheses regarding the brain basis of personality disorders, where atypical social cognition can be manifested as a key symptom (Lis and Bohus, 2013). While fMRI data on how personality influences brain processing of social stimuli are scarce to date, there is some emerging evidence that the amygdala, as well as the RTCS, react more strongly to facial expressions as a function of extraversion (Canli et al., 2002; Suslow et al., 2010). In addition, one fMRI study has found that activity in the ventromedial prefrontal cortex and ventral striatum is associated with extraversion during a social multi-player task (Morawetz et al., 2014). Finally, two fMRI investigations report that activity in the temporal pole is associated with neuroticism during (i) the processing of sad faces and (ii) within the context of a false belief paradigm (Jimura et al., 2010, 2009). Despite such initial evidence on brain activity linked to social processing as a function of personality, studies testing the fundamental dissociation between social versus nonsocial stimulus content are still lacking.

1.4. Our approach

Here, for the first time, we examined how differences in personality traits (specifically extraversion and neuroticism) affect the processing of dynamic and natural gestures containing social versus nonsocial intent. To accomplish this goal, we use a recently developed fMRI-based dynamic social gestures (DSG) task, which permits studying multiple aspects (e.g., face-visibility and actororientation) of a social interaction (Saggar et al., 2014). The DSG task uses dynamic and natural gesture stimuli (video clips of 2 s each) in an event-related fMRI design. The task can be used to assess three aspects of interaction - sociability, actor-orientation, and face-visibility. For sociability, gestures that are intended to elicit a response (e.g., a friendly wave) were deemed as social in nature, while other gestures (e.g., reaching for a cup) were deemed nonsocial. The second aspect, actor-orientation, was used to assess differences in neural mechanisms associated with personal engagement (i.e., when the actor in the clip is facing the participant) versus with passive observation (i.e., when the actor is looking at a third person; not shown in the clip). Finally, the third aspect of face-visibility (i.e., actors' face blurred versus visible) was included in the task to assess whether facial information itself is the primary driver of neural activation while processing social versus nonsocial gestures (Saggar et al., 2014).

Enhanced reward sensitivity is considered to be the source of higher sociability in extraverts (Lucas et al., 2000), and previous research suggests a role of extraversion during reward learning (Hooker et al., 2008). Therefore, we hypothesized that while processing social (versus nonsocial) gestures extroverts would have increased activity in reward-related brain areas (e.g., orbitofrontal cortex, ventral striatum and amygdala). Further, based on the work by Eysenck, other researchers have argued that extroverts may have lower levels of reticulothalamic-cortical arousal, and therefore a higher neural threshold for arousing stimuli (Eysenck, 1997, 1994; Suslow et al., 2010). Additionally, extraversion has been behaviorally linked with experiences of excitement and positive affect particularly during social interactions (Hutcherson et al., 2008; Lucas et al., 2000). Consequently, we also predicted extraversion to be associated with higher activity in the RTCS during social as compared to non-social gestures. Finally, neurotic individuals are generally thought to show over-reactive or instable limbic brain region activation to emotionally arousing information (Jimura et al., 2009; Kehoe et al., 2012). We hypothesized that for individuals with higher neuroticism scores, perceiving a gesture that intends to elicit a response (i.e., a social gesture) would be

emotionally arousing and would in turn be associated with increased activity in the "emotional brain".

2. Materials and methods

2.1. Participants

Twenty healthy young adults (average age=21.41, SD=2.36, range=16.9–25.7 years; 10 female) participated in this study after giving written informed consent. All subjects were right-handed, had no contraindications for MRI scanning (e.g., metal implants or pacemakers), and had no self-reported history of past or current psychiatric or neurological condition. The university's research ethics board approved the experimental protocol and procedures.

2.2. Behavioral testing

In an initial testing session prior to scanning, participants completed self-report measures of personality traits. We used the NEO Personality Five Factor Inventory scale (NEO-FFI; PAR: http://www3.parinc.com/), which provides a short and reliable measure of the five domains of personality (neuroticism, extraversion, openness, agreeableness and conscientiousness). For each NEO subscale, *gender-specific T*-scores were calculated, demeaned and used as covariates during the neuroimaging analyses. In addition to extraversion and neuroticism, the three factors of openness, agreeableness, and conscientiousness scores of the FFM were also included in the analysis to control for possible inter-correlations and in turn to examine contributions unique to extraversion and neuroticism.

2.3. Task and stimuli

We used the previously developed dynamics social gestures (DSG) task (Saggar et al., 2014). The DSG task was designed to investigate the neural networks associated with processing of naturalistic and dynamic gestures with a social versus nonsocial intent, with added factors for actor-orientation and face-visibility (see Saggar et al. (2014) for more details). Briefly, the DSG task comprised of a set of short (2s) color video clips of live actors either performing a social gesture ("friendly wave," "handshake," "beckoning," "joint attention," or "imploring") or a nonsocial gesture ("rubbing hand on table," "reaching for a cup," "brushing off a table," "looking at a book," and "looking at arms"), with comparable overall amount and direction of movement and appropriate valence.

Additionally, to understand how the human brain differentially processes gestures with respect to personal engagement during a social interaction versus passive observation of an action, a factor of actor orientation was included in the DSG task. Thus, in half of the clips, actors directly faced the participant ("towards" or "personal engagement" condition), and in the other half of the clips actors were turned at an angle, as if they were addressing an unseen individual just off camera ("away" or "passive observation" condition).

Lastly, to elucidate the neural correlates of naturalistic social interactions, actors were instructed to portray facial expressions associated with the performed gesture. Thus, a third factor of face-visibility (i.e. actor's faces were visible versus blurred) was added to the DSG task to test whether the facial information itself were the *primary driver* of neural activation differences between social and nonsocial gestures. Thus, our stimuli comprised a 2 (*sociability*: social versus nonsocial) \times 2 (*actor-orientation*: towards versus away) \times 2 (*face-visibility*: visible versus blurred) factorial design, with 25 stimuli in each of these 8 experimental conditions

(200 different stimuli in total). These stimuli were not equated for the amount of motion or motion energy across conditions.

Participants viewed all movie clips during two runs (approximately 16 min in total) and, as an attentional cover task, were asked to press a button with their right index finger when they saw a red dot appear near the actors' eyes and nose. Red dots appeared on half of the gestures 1 s after the clip onset, and were equally likely to occur in every condition. This cover task was designed to be a simple control to ensure that participants were paying attention to the stimuli and were kept naïve to the hypotheses of the study. As reported previously (Saggar et al., 2014), participants achieved near-perfect accuracy in the cover task (M=98.75%, SD=1.9%).

2.4. MRI acquisition

Participants were scanned on a 3 T (GE Signa scanner, Milwaukee, WI) MRI at Stanford's Lucas Center for Neuroimaging using a custom-built single-channel birdcage head coil optimized for fMRI scans. Over two runs, a total of 469 whole-brain volumes were collected on 30 axial-oblique slices (4.0 mm thick, 1.0 mm skip) prescribed parallel to the intercommissural (AC-PC) line, using a T2*-weighted gradient echo spiral pulse sequence sensitive to blood oxygen level-dependence (BOLD) contrast with the following acquisition parameters: Echo Time (TE)=30 ms, repetition time (TR)=2000 ms, flip angle=80°, FOV=22 cm, acquisition matrix= 64×64 , approximate voxel size= $4.0 \times 3.4 \times 3.4$ mm³. To reduce blurring and signal loss arising from field in-homogeneities, an automated high-order shimming method based on spiral acquisitions was used before acquisition of functional MRI scans. A high-resolution T1-weighted three-dimensional inversion recovery spoiled gradient-recalled acquisition was acquired for coregistration with the following parameters: Echo Time (TE)=6 ms, repetition time (TR)=35 ms, flip angle= 45° , FOV=24 cm, slice thickness = 1.5 mm, 124 slices in the coronal plane; matrix= 256×192 ; acquired resolution= $0.94 \times 1.25 \times 1.5$ mm³. The images were reconstructed as a $256 \times 256 \times 124$ matrix.

2.5. fMRI analysis

Functional MRI data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The following pre-statistics processing was applied: motion correction using MCFLIRT, non-brain removal using BET, spatial smoothing using a Gaussian kernel of FWHM 5 mm, grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, and highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 120.0 s). Additionally, sharp motion peaks were detected using *fsl_motion_outliers* script (supplied with FSL) and were regressed out in addition to the six motion parameters (from MCFLIRT). Registration to high-resolution structural and standard space images was carried out using FLIRT. Time-series statistical analysis was carried out using FILM with local autocorrelation correction. Intra-subject individual runs were combined using a fixed effects model, by forcing the random effects variance to zero in FLAME (FMRIB's Local Analysis of Mixed Effects). Group-level analysis was carried out using FLAME (FMRIB's Local Analysis of Mixed Effects) stage 1 with automatic outlier detection. Group-level analysis was cluster corrected at Z > 2.3, p < 0.05. Additionally, we applied an overall correction across the seven neuroimaging contrasts using the False Discover Rate (FDR) method of multiple comparisons correction (Table 1) (Benjamini and Hochberg, 1995). Gender-specific scores of the five NEO-FFI factors were demeaned and used as covariates at the group level in a single multiple regression analysis. Featquery tool (supplied by

Table 1

Local maxima locations (in TAL and MNI space) and associated statistics for each cluster.

Cluster num.	Z-value	Cluster size	FDR-corrected <i>p</i> -value	TAL coordinates			MNI coordinates			Hemisphere	Region
				X coor	Y coor	Z coor	X coor	Y coor	Z coor		
Extraversion a	nd sociabil	ity									
1	3.24	501	0.0137	-4.9	-14.26	2.3	$^{-4}$	-14	0	L	Thalamus
	3.23			6.45	- 16.26	2.24	8	- 16	0	R	Thalamus
	3.11			- 12.48	- 16.09	2.14	-12	- 16	0	L	Thalamus
	3.01			6.41	-25.85	3.43	8	-26	2	R	Thalamus
	3			0.8	-8.62	2.71	2	-8	0	L	Thalamus
	2.95			19.63	-31.77	4.93	22	-32	4	R	Thalamus
Neuroticism a	nd interact	ion between ac	tor-orientation and face-v	isibility							
2	3.22	662	0.0091	- 37.05	-1.06	8.39	- 38	0	6	L	Insula
	3.11			-48.41	-4.52	4.48	-50	-4	2	L	Superior Temporal Gyru
	3.04			-48.39	-0.72	4.73	-50	0	2	L	Superior Temporal Gyru
					-0.33	-0.71	- 56	0	$^{-4}$	L	с : т I.С
	2.98			- 54.06	-0.55	0.71	00				Superior Temporal Gyru
	2.98 2.94			- 54.06 - 27.62	- 12.4	5.9	-28	- 12	4	L	Lentiform Nucleus
								-12 -22	4 6	L L	
1	2.94	536	0.0137	-27.62	-12.4	5.9	-28				Lentiform Nucleus
1	2.94 2.81	536	0.0137	-27.62 -27.66	- 12.4 - 21.99	5.9 7.09	-28 -28	-22	6	L	Lentiform Nucleus Lentiform Nucleus
1	2.94 2.81 3.22	536	0.0137	-27.62 -27.66 31.14	- 12.4 - 21.99 9.84	5.9 7.09 7.71	-28 -28 34	-22 12	6 4	L R	Lentiform Nucleus Lentiform Nucleus Claustrum
1	2.94 2.81 3.22 2.97	536	0.0137	-27.62 -27.66 31.14 29.27	- 12.4 - 21.99 9.84 17.44	5.9 7.09 7.71 8.2	-28 -28 34 32	-22 12 20	6 4 4	L R R	Lentiform Nucleus Lentiform Nucleus Claustrum Claustrum
1	2.94 2.81 3.22 2.97 2.87	536	0.0137	-27.62 -27.66 31.14 29.27 25.44	- 12.4 - 21.99 9.84 17.44 - 4.47	5.9 7.09 7.71 8.2 - 5.92	-28 -28 34 32 28	-22 12 20 -4	6 4 4 - 10	L R R R	Lentiform Nucleus Claustrum Claustrum Lentiform Nucleus

FSL) was used to extract percent change in parameter estimates in the regions of interests masked by functional activity. MRIcron (http://www.mricro.com/) was used to visualize neuroimaging results on the standard anatomical brain.

2.6. Reporting results

In addition to reporting the coordinates for the peak voxel within each cluster, we also report 5 local maxima values (reflecting the spatial extent of each cluster). These local maxima locations were defined as those voxels whose surrounding voxels are all of lower intensities (extracted using the –olmax option in FSL's cluster command; http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Cluster). The local maxima values are reported in Table 1 in descending order (i.e., second from peak, third from peak and so on).

Although we used the MNI-152 average brain for group-level analysis, we also report the final results in Talaraich coordinates (TAL), for consistency with our previous study (Saggar et al., 2014). The conversion from MNI to TAL was accomplished using GingerALE 2.3 (http://www.brainmap.org). GingerALE uses the spatial transform called icbm2tal (with parameters specific to FSL).

3. Results

3.1. Behavior

The descriptive statistics for the gender-specific NEO-FFI T-scores in our sample are as follows, neuroticism: mean=49.85, SD=10.78; extraversion: mean=52.25, SD=10.15; openness: mean=58.20, SD=10.18; agreeableness: mean=49.80, SD=13.19; conscientiousness: mean=46.80, SD=12.43. Extraversion scores were positively correlated with agreeableness (r=0.461, p=0.04), but negatively correlated with neuroticism at a trend statistical level (r= -0.424, p=0.06). Agreeableness scores were also positively correlated with openness (r=0.655, p=0.002). There were no other significant correlations between the FFI scores (|r| < 0.35, p > 0.1). Further, no signification correlations were found between participants' age and the FFI scores (|r| < 0.45, p > 0.05). These

correlations are consistent with previously published findings (see for example Liu et al. (2013)).

3.2. Neuroimaging

To examine the influence of personality measures on DSG processing, all five gender-specific NEO T-scores were used as covariates (multiple regression analysis to control for possible interrelations), while contrasting for the three main effects (sociability, actor-orientation, and face-visibility) and four interactions between the main factors (sociability × actor-orientation; sociability × face-visibility; actor-orientation × face-visibility; and sociability × actor-orientation × face-visibility). Significant effects for extraversion and neuroticism, after controlling for openness, agreeableness, and conscientiousness, are reported below.

3.2.1. Effect of extraversion

For the main effect of sociability, i.e. contrasting gestures with social versus nonsocial intent, extraversion was found to significantly influence BOLD signal change in the thalamus, extending into the right hippocampus (Fig. 1A and Table 1). To visualize and further specify the directionality of the observed extraversion effect, percentage beta-estimates were extracted from all significant voxels of the thalamus cluster for each participant, averaged, and fed to multiple regression analysis with all the five FFI scores. As evident from the partial regression plot (Fig. 1B), this analysis revealed that participants with higher extraversion scores had higher differential thalamus activation for processing gestures with social as compared to nonsocial intent. No other effects of extraversion were observed for any other contrast.

3.2.2. Effect of neuroticism

Neuroticism scores were observed to influence the BOLD signal change reflecting interaction between the factors of actor-orientation and face-visibility in two separate activation clusters (Fig. 2A and Table 1). These clusters encompassed regions in the bilateral frontal operculum and insula (fO/I), extending into the right amygdala, bilateral putamen, and left superior temporal gyrus (STG). To visualize and further examine the directionality of

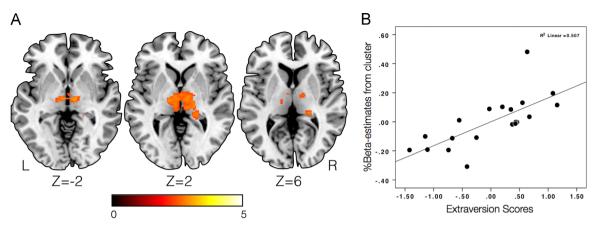


Fig. 1. Effect of extraversion on sociability. (A) Influence of extraversion on the contrast of processing gestures with social versus nonsocial intent. The cluster encompasses bilateral thalamus and right hippocampus. Activations are overlaid on the MNI-152 average brain. Color bar represent cluster-corrected Z-stats at FWE p < 0.05. (B) Partial regression plot visualizing the direction of effect. Participants with higher extraversion scores had higher differential activation during social as compared non-social gesture processing. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

these effects, percentage beta-estimates were extracted from all significant voxels of the bilateral fO/I clusters for each participant, averaged, and fed to multiple regression analysis with all the five FFI scores. The partial regression plots (Fig. 2B and C) show that neuroticism scores specifically moderated the interaction between actor-orientation and face-visibility in the left and right fO/I regions, such that participants with higher neuroticism scores had higher activity when actors were oriented away from them (as compared to oriented towards them) or when the actor's face was

visible (as compared to blurred). No other effects of neuroticism were observed for any other contrast.

4. Discussion

We investigated the influence of extraversion and neuroticism on cognitive affective processing underlying dynamic and natural social versus nonsocial gesture perception. We predicted that

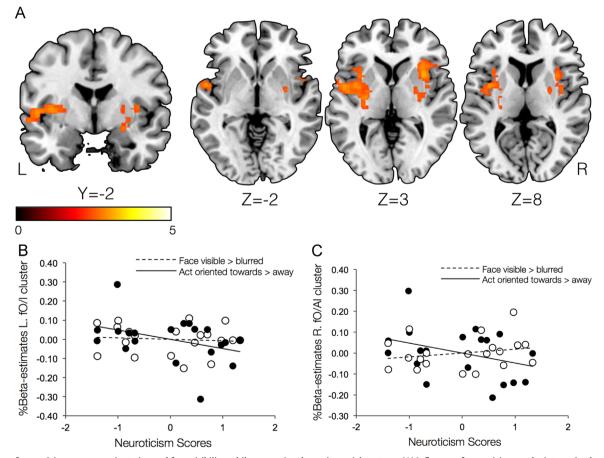


Fig. 2. Effect of neuroticism on actor-orientation and face-visibility, while processing dynamics social gestures. (A) Influence of neuroticism on the interaction between actororientation (act oriented towards versus away) and face-visibility (actor's face visible versus blurred). The clusters mainly encompass frontal operculum, insula, and superior temporal gyrus. Activations are overlaid on the MNI-152 average brain. Color bar represent cluster-corrected Z-stats at FWE p < 0.05. (B, C) Partial regression plots visualizing the direction of effect for the bilateral fO/I clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

while processing social interactions, participants with higher scores on the extraversion scale would have higher activity in the reward-related areas and/or the reticulothalamic-cortical arousal system (RTCS). We also anticipated that participants with higher scores on the neuroticism scale would have higher activity in the limbic brain regions, reflecting over-reactivity or instability during the processing of arousing information. The obtained findings partly support our hypotheses. We found a positive correlation between bilateral thalamic activity and extraversion scores during the processing of social (versus nonsocial) gestures. For neuroticism, the brain activation data revealed a more complex pattern. Here, activity in the "emotional brain" (comprising bilateral frontal operculum and insula, further extending into bilateral putamen and right amygdala) was moderated as a function of actor-orientation (towards versus away from participants) and face-visibility (actor faces visible versus blurred). The above findings and their implications in relation to extraversion and neuroticism personality traits are discussed more in detail below.

4.1. Extraversion

For the main contrast of sociability, i.e., contrasting social versus nonsocial gestures, we observed a positive relation between BOLD signal in the bilateral thalamus (extending into the right hippocampus) and extraversion scores. In other words, our data revealed that for participants with higher scores on extraversion, activity in a central component of the RTCS was higher for gestures with a social (versus nonsocial) intent. Such activation pattern accords with more pronounced social approach tendencies generally associated with extraversion. It has been argued that such approach tendencies likely bias individuals to look for arousing experiences that are related to reward (or its expectation) within a social context (DeYoung et al., 2010).

In previous fMRI investigations, examinations of individual differences in arousal responses as a function of extraversion were largely limited to emotional valence. For example, Canli and colleagues examined how extraversion and neuroticism influence brain activity related to processing of happy versus angry faces (Canli et al., 2002). Similarly, Kehoe and colleagues used positive and neutral images from the International Affective Picture System, and Mobbs et al. used humorous (or positive) versus neutral cartoons, to examine how personality influences brain processing of emotional stimuli (Kehoe et al. 2012; Mobbs et al., 2005). In contrast to using emotional valence, here we employed different factors of social interaction like sociability, actor-orientation (or first versus third person perspective), and face-visibility. We argue that these factors, in addition to valence, could significantly drive the arousal-seeking behavior associated with extraversion. Our data thus provide preliminary evidence that extraversion may increase neural sensitivity to social (versus nonsocial) information in the RTCS. Such engagement of the RTCS may facilitate processing of social intent in individuals with higher extraversion scores.

Our results, however, do not support Eysenck's theory of extraversion, which proposes decreased sensitivity to arousing information due to chronic under-arousal of the RTCS (Eysenck, 1994, 1963). Supporting this notion, Kehoe et al. (2012) have recently challenged Eysenck's concept of extraversion by stating that "the relationship between extraversion and arousal is not as simple as that proposed by Eysenck" (p. 866). This may particularly hold true for healthy populations with extraversion scores in a normal, subclinical, range. Despite the fact that such healthy populations appear to be characterized by chronic neural underarousal of the RCTS at baseline (see i.e., Hagemann et al. (2009), Kumari et al. (2004)), extraversion still seems to enhance arousalrelated brain responses as a function of positive stimulus valence (Kehoe et al., 2012), or social intent as shown here. Future investigations that can systematically distinguish brain activity to (a) social versus nonsocial, (b) positive versus neutral (and negative), and (c) low versus high arousing stimulus properties, as a function of extraversion, are needed to elucidate the relationship between extraversion and arousal-related brain activity during social cognitive affective processing.

4.2. Neuroticism

We observed neuroticism scores to be associated with BOLD signal activity reflecting an interaction between the factors of actororientation and face-visibility. Specifically, we found a negative association between neuroticism scores and actor-orientation, and a positive association between neuroticism scores and face-visibility in the "emotional brain" (comprising bilateral frontal operculum and insula, further extending into bilateral putamen and right amygdala). Thus, high neuroticism was related to stronger brain activity during exposure to the gestures performed away (versus towards) from participants, and containing visible (versus blurred) faces.

Neuroticism is generally described as an over-reactivity or instability of the "emotional brain" (Dalgleish, 2004). In particular, neurotic individuals show such instability while processing negatively valenced and/or emotionally arousing information (Jimura et al., 2009; Kehoe et al., 2012) associated with threat or punishment (DeYoung et al., 2010). Neuroticism has also been shown to modulate emotional brain processes associated with successfully understanding another person's mental states (Jimura et al., 2010). Accordingly, our data may suggest that participants with high neuroticism scores experienced increased negative emotional arousal while processing gestures performed away from them with the actor's face visible. One possible conjectural interpretation of these data may be that gestures performed away from the participants were perceived as conflicting or unexpected, and may have signaled social rejection/exclusion and a social threat. Such interpretation is corroborated by previous fMRI findings, which show engagement of the insula, amygdala and putamen in social conflict perception and rejection paradigms (Kross et al., 2007; Lamm and Singer, 2010; Silk et al., 2014; Zucker et al., 2011). Our interpretation also accords with a general model of emotion processing in neuroticism derived from a quantitative meta-analysis of neuroimaging studies (Servaas et al., 2013). In this general model, neuroticism is linked to a negative processing bias that is thought to result in an increased tendency to appraise the world as more threatening. Such negative processing bias is corroborated by a previous finding that neuroticism represents a risk factor for social phobia and agoraphobia (Bienvenu et al., 2007). Applied to the present paradigm, it may therefore be that healthy individuals with higher neuroticism scores perceived gestures with a visible face performed away from them as more negative in terms of social conflict, rejection and/or threat. However, future studies are necessary to replicate and further extend these preliminary findings, particularly pertaining to social versus nonsocial information processing and how these different conditions relate to arousal.

Although robust correlations with brain activity were observed for both extraversion and neuroticism, the overall mean activation levels (across participants) might sum up to zero. For example, while perceiving social gestures, some brain regions (e.g., the thalamus) were found to be more engaged (or disengaged) based on individual personality scores, although no mean activations for the sociability contrast were observed across the entire sample of participants (see our previous paper reporting on mean activations; (Saggar et al., 2014)). Thus, the observed personality correlations described here bolster our overall claim that personality should be taken into account while examining the neural correlates of social gesture processing in particular, and social stimuli processing in general.

5. Limitations

In designing the DSG task, we intentionally avoided fine fragmentation of gesture stimuli into previously conceptualized categories (e.g., "transitive" versus "intransitive" (Villarreal et al., 2008) or "expressive" versus "instrumental" gestures (Gallagher and Frith, 2004)). Although such fragmentation provides crucial and specific information regarding cognitive affective processing of particular types of gestures, it also inadvertently hinders the development of a holistic understanding of the complexities of natural social information processing. As a first step towards such understanding, we broadly conceptualized gestures into the dichotomy of social versus nonsocial categories. However, future work is required to examine whether dividing gestures into overarching categories (even as broad as social versus nonsocial) versus studying them in a continuum is going to provide a better holistic understanding of social information processing.

Additionally, as opposed to controlling for the valence, actors in the DSG task were instructed to portray the facial expressions in accord with the nature of gesture being performed. This choice allowed studying of social gestures in a natural state, but it also obstructed delineation of the effects of valence from that of sociability. Future investigations that systematically vary the three dimensions of sociability, valence, and arousal are needed to examine the relationship between personality traits and arousalrelated brain activity during social cognitive affective processing.

We are also aware of the fact that gestures only represent one element of naturally occurring social interactions. Additional elements include linguistic behavior, prosody, etc. In order to fully understand how personality, and particularly extraversion and neuroticism, relate to social (versus nonsocial) brain activation, future investigations probing different elements of social interactions are required.

Finally, we would like to point to the fact that the present study included a relatively small sample of N=20 participants. Although we applied a conservative statistical threshold for our whole-brain multiple regression contrasts and performed an additional FDR correction to account for multiple comparisons, our results should be understood as preliminary until further extended and replicated.

6. Conclusion

Our fMRI investigation, for the first time, examined the influence of two well-known personality traits, extraversion and neuroticism, on brain activity associated with processing of natural and dynamic social gestures. In contrast to previous work, which focused largely on emotional valence, we studied the effects of personality directly on the factors of sociability, actor-orientation and face-visibility during cognitive-affective processing. In so doing, we found that higher extraversion scores were associated with stronger activation of the thalamus, a brain region belonging to the reticulothalamic-cortical arousal system, during the processing of social (versus nonsocial) gestures. Higher neuroticism scores were associated with increased BOLD signal change predominantly in the "emotional brain" while participants perceived gestures performed away from (versus towards) them with a face visible (versus blurred). Such findings point towards the existence of factors other than emotional valence influencing social gesture processing in particular, and social cognitive affective processing in general, as a function of personality. Future studies including further differentiation of social stimuli in terms of valence and arousal, in addition to the three factors employed here, are highly encouraged.

Conflict of interest

The authors declare no competing financial interests.

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