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The trait of sensory processing sensitivity and neural responses to changes in visual scenes

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This exploratory study examined the extent to which individual differences in sensory processing sensitivity (SPS), a temperament/personality trait characterized by social, emotional and physical sensitivity, are associated with neural response in visual areas in response to subtle changes in visual scenes. Sixteen participants completed the Highly Sensitive Person questionnaire, a standard measure of SPS. Subsequently, they were tested on a change detection task while undergoing functional magnetic resonance imaging (fMRI). SPS was associated with significantly greater activation in brain areas involved in high-order visual processing (i.e. right claustrum, left occipitotemporal, bilateral temporal and medial and posterior parietal regions) as well as in the right cerebellum, when detecting minor (vs major) changes in stimuli. These findings remained strong and significant after controlling for neuroticism and introversion, traits that are often correlated with SPS. These results provide the first evidence of neural differences associated with SPS, the first direct support for the sensory aspect of this trait that has been studied primarily for its social and affective implications, and preliminary evidence for heightened sensory processing in individuals high in SPS.

Keywords: sensory processing sensitivity; temperament; personality; fMRI; visual processing; highly sensitive person scale

INTRODUCTION

Sensory processing sensitivity (SPS) is a temperament/personality trait characterized by sensitivity to both internal and external stimuli, including social and emotional cues. The standard measure of SPS in adults is the 27-item Highly Sensitive Person Scale (HSP Scale), validated using a variety of methods and populations (Aron and Aron, 1997). Items include being aware of subtleties, bothered by intense stimuli and strongly affected by caffeine, pain and time pressures; startling easily, being more aware of others' moods; and performing poorly when observed (due to over arousal).

The SPS concept adopts the view from biology that most species have evolved 'personality' types; for example, shy or bold, aggressive or nonaggressive and sensitive or not (Sih and Bell, 2008); that represent two underlying strategies. One is 'pausing before acting' (or being 'responsive': Wolf *et al.*, 2008) in order to allow neural processes to assess survival-related subtleties in the environment. The other is 'acting first' so as to respond quickly to opportunities and discover survival-relevant cues through motor exploration. For example, in fruit flies, there are two types, sitters and

rovers, representing two strategies of locating food (Renger *et al.*, 1999).

These two types determine behaviors such as feeding, harm avoidance, mating, affiliating and seeking higher status. The two strategies remain, because they each can succeed under different but normal variations in habitat (Wilson *et al.*, 1993; Sih and Bell, 2008).

SPS is closely related behaviorally to traits characterized by pausing before acting. These include behavioral inhibition (Carver and White, 1994; Kagan *et al.*, 1994), shyness (Jones *et al.*, 1986), introversion and neuroticism (Aron and Aron, 1997) and, most recently, biological sensitivity to context (Ellis *et al.*, 2005).

High-behavioral inhibition is usually interpreted as a greater sensitivity to punishment or threat (Carver and White, 1994), resulting from an especially active behavioral inhibition system (BIS). As originally conceived, greater behavioral inhibition was associated with a strategy of taking time to process stimuli more thoroughly, especially in novel situations, whether these were threatening stimuli or not (Gray, 1981, 1986). While the point is often missed, Gray did not view behavioral inhibition as only a greater awareness of the threat of punishment. Indeed, Gray's revised model (McNaughton and Gray, 2000) makes the BIS a mediator between the urge to proceed, coming from the BAS and the fear system in the amygdala.

Aron and colleagues (2005) found support in four studies for a model in which the interaction of SPS and a troubled childhood predicted negative affectivity/neuroticism.

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Liss and colleagues (2005) found a similar interaction which, in turn, predicted shyness. These findings suggest that shyness, as a reason for pausing before acting, is related to sensitivity but not identical to it.

Introverts have been found to have a greater awareness of subtle stimuli, more attentional vigilance (Koelega, 1992) and greater sensory reactivity (Stelmack, 1990; Doucet and Stelmack, 1997, 2000). Introversion has been related to reflectivity, defined as a slow and accurate response style (Kagan *et al.*, 1964) and a contemplative cognitive process (Patterson *et al.*, 1987). Compared to extraverts, introverts respond more slowly following a punished trial and evidence learning more from it (Patterson *et al.*, 1987), all of which suggests a preference for more elaborate processing of stimuli.

We suggest that, in humans, learning history interacts with the sensitive, pausing-first-to-observe strategy to create a range of social behaviors (from leadership to withdrawal) and emotional valences (from negative to positive). This would explain moderate correlations of the HSP Scale with introversion and neuroticism (Aron and Aron, 1997). In the case of introversion, we suspect that some, but not all, of those high in SPS have learned to avoid sensory overload, a self-reported problem on the HSP Scale, by choosing interactions with intimates over meeting strangers or being in large groups. Regarding neuroticism or negative affectivity, as noted earlier, there is some evidence (Aron *et al.*, 2005) that those higher in SPS have stronger emotional responses overall, but the type of affect is determined by life history. Indeed, with good parenting, sensitive or 'emotionally reactive' children are healthier (Ellis *et al.*, 2005) and 'reactive' primates more likely to be troop leaders (Suomi *et al.*, 1991) compared to those without the trait.

As previously mentioned, individuals with traits related to SPS are characterized by a reflective response style (Patterson *et al.*, 1987). Additionally, individuals high in SPS report having rich, complex inner lives, as well as noticing subtleties in their environment (Aron and Aron, 1997), all of which suggests they process stimuli more elaborately and/or pay more attention to stimuli.

Given the above, the present study investigated the relationships between SPS and the perceptual and cognitive processes underlying the tendency to pause before acting. Specifically, we investigated the possibility that individuals high in SPS pay more attention to stimuli and/or process stimuli more elaborately. That is, we investigated the extent to which individual differences in SPS are associated with neural activation in primary, secondary and high-order visual areas in response to gross *vs* subtle changes in visual stimuli.

Sensory information is transformed into cognition by associative elaboration modulated by attention (Mesulam, 1998). The processing of visual information, specifically, takes place by means of neural networks ranging in complexity from unimodal areas encoding features of sensation

through to transmodal areas such as the limbic and paralimbic areas, which integrate information from the unimodal areas (Mesulam, 1998). Attention is critical for noticing change (Rensink *et al.*, 1997; Kelley *et al.*, 2003) and can be measured using a change detection task (Rensink, 2002) in which the participant is shown a stimulus, then the stimulus is changed, and the behavioral response to the change is measured, generally in terms of response time (Rensink, 2002).

Neuroimaging has been increasingly used to investigate individual differences. The majority of studies have investigated the relationship between differences in personality or temperament and cognition or emotion (e.g. Gray and Braver, 2002; Canli *et al.*, 2004; Henderson and Wachs, 2007). Although a few researchers (Childers and Jiang, 2008; Sergerie *et al.*, 2008) have studied individual differences in sensory perception/processing, the literature is not a large one, nor does it address differences in personality/temperament. The conceptualizations reviewed above suggest that the way sensory information is processed is the key to the temperamental difference characterized as SPS and related constructs. This investigation is the first to examine the brain mechanisms that might underlie such a difference.

In our study, participants compared a photograph of a visual scene with a preceding scene and indicated, with a button press, whether the scene had changed from the preceding scene. The primary manipulated variable was level of detail of change (major/minor) in visual scenes; as an additional exploratory variable, we also manipulated speed of presentation (fast/slow) of the scenes. Since the study was exploratory with respect to neural activation, we did not have specific hypotheses. However, we asked the following research questions: 'Will there be a relationship between SPS and brain activation in response to subtle changes in visual stimuli?' and 'If there are differences between individuals high and low in the trait, what specific brain regions will show these differences?'

METHODS

Participants

Participants were 18 healthy, right-handed students with normal or corrected-to-normal vision. They were a sample of convenience recruited from the Chinese Agricultural University, Beijing Normal University and Peking University, all in Beijing, China. Participants gave informed consent. All procedures were approved by the Institutional Review Boards at the Chinese Academy of Sciences, where the scanning took place, and at Stony Brook University. Imaging data from two participants had to be discarded due to scanner error. The remaining 16 participants (8 women) were 19–25 years old ($M = 21.6$, $s.d. = 1.63$). Mean SPS was 5.00 ($s.d. = 0.60$), somewhat higher than two recent U.S. samples (3.88, 4.33; $s.d.s$, 0.58, 0.83) recruited in about the same way, which we have studied

for other purposes. This higher mean is probably due to our participants being more comfortable giving somewhat higher ratings to scale items, because Chinese cultural norms appear to be relatively more positive about sensitivity (Chen *et al.*, 1992). However, we have no reason to believe North Americans would show a different association of SPS with response to our task.

Stimuli

Stimuli were 16 black and white original photographs of natural and man-made scenes (see Figure 1 for example). Each photograph was also altered with either a major change or a minor change using Photoshop software. Major changes consisted of easily noticeable alterations (e.g. inserting a second fencepost into a prominent fence); minor changes, of more subtle alterations (e.g. inserting half a hay bale in front of an existing line of hay bales). Stimuli were pilot-tested to be sure pilot subjects could detect both major and minor changes presented both quickly and slowly.

Questionnaire measures

SPS was measured using 26 items from the 27-item HSP Scale (Aron and Aron, 1997), translated into Chinese (by two graduate students at The Chinese Academy of Sciences) and then back-translated (by two different graduate students) into English to ensure accuracy of translation. Discrepancies were resolved by discussion among the four graduate students. One item was omitted from the scale due to clerical error. The HSP Scale has been shown to have strong discriminant and convergent validity (Aron and Aron, 1997) as well as good internal consistency. Cronbach's alphas in previous studies have typically been 0.85 or higher (e.g. Aron and Aron, 1997; Aron *et al.*, 2005; Benham, 2006; Hofmann and Bitran, 2007).

Alpha in this study was 0.77. (Note that our slightly lower alpha works against getting significant correlations.) Example items are 'Are you deeply moved by the arts or music?', 'Do other people's moods affect you?', 'Do you seem to be aware of subtleties in your environment?', 'Are you easily overwhelmed by strong sensory input?', and 'Do you startle easily?'

Neuroticism and introversion were measured with a 50-item short form of the NEO Personality Inventory—Revised (NEO-PI-R; Costa and McCrae, 1992) translated and back-translated as per the HSP Scale procedure. The NEO-PI-R is a valid and widely used measure of the 'Big Five' normal personality traits. However, in the present context, we were able to use only a subset of items for each of our focal scales. Due to clerical errors, only 50 of the usual 60 items were administered. Additionally, subsequently discovered translation errors eliminated some of the items we did have, and testing of the items that seemed reasonable showed that a few actually reduced the alpha. The final scales we used included four items each. For neuroticism, these were NEO-PI-R items 8, 10, 36 and 47 ($\alpha = 0.62$).

Example items: 'I often worry about things that might go wrong' and 'Frightening thoughts sometimes come into my head'. For introversion, these were items 3, 19, 29 and 31 ($\alpha = 0.44$). Example items: 'I shy away from crowds of people' and 'I prefer jobs that let me work alone without being bothered by other people'.

Correlations of neuroticism and introversion with the HSP Scale were 0.10 (*n.s.*) and 0.16 (*n.s.*), respectively. These are lower than previous correlations found in North American samples (Aron and Aron, 1997), possibly because the measures were weaker due to translation issues. Also, this discrepancy could be due, as noted earlier, to sensitivity being more highly valued in Chinese societies, so that sensitive individuals are not seen as introverted or neurotic.

Design and procedure

The task was adapted from a change detection task used by Rensink and colleagues (1997). Stimuli were presented in 16 blocks, comprising 72 image presentations in total. Each block contained images with either minor changes or major changes presented either slowly or quickly. Blocks of quickly presented stimuli (i.e. fast condition) consisted of five (i.e. one original, four target) images presented for 1.20 s each. The four target images were separated by fixation crosses of 4.79 s (see Figure 2). Blocks of slowly presented stimuli (i.e. slow condition) consisted of four (i.e. one original, three target) images presented for 2.0 s each. Target images were separated by fixation crosses of 4.0 s. Conditions were presented in random order, and images were presented in random order within each condition.

When viewing the images, participants performed a change detection task while in a functional magnetic resonance imaging (fMRI) scanner, indicating their responses by pressing buttons on a button box. While in the scanner, a participant viewed a fixation cross, the original image, then the same image changed or unchanged from the preceding image, with fixation crosses between each image. The participant was instructed to respond during the fixation crosses, starting in each block during the fixation cross following the second image. The participant pressed the left button to indicate the image was the same as, and the right button to indicate the image was different from, the preceding image. After the initial image, on average, half the images in each block were the same, and half different, from the preceding image.

Visual stimuli were projected on a screen placed directly outside the MRI tube, subtending a visual angle of 17°. Participants viewed images via an angled mirror mounted on the RF coil of the scanner. The participants were presented with a box containing two response buttons connected to a personal computer running Eprime software (Version 1.0, Psychology Software Tools, Pittsburgh, PA, USA).

We acquired functional images on a 3T GE Signa LX MRI scanner (General Electric, Waukesha, WI, USA) at



Fig. 1 Example of (A and B) original stimuli, (C) stimulus with a major change and (D) stimulus with a minor change.

the Beijing MRI Center for Brain Research and recorded blood oxygen level-dependent responses. We acquired functional images using T2-weighted gradient-echo echo-planar sequence (repetition time 2000 ms, echo time 30 ms, 90° flip angle, field of view 240 × 240 mm, 64 × 64 matrix). The images consisted of 30 contiguous axial slices of 4-mm thickness. Voxel size was 3.8 × 3.8 × 4.00 mm. Four volumes were introduced before beginning the set of blocks for the experiment and discarded from analysis. Not including the four discarded volumes, 218 volumes were acquired during the

7.2-min functional scan. We also acquired anatomical, axial T1-weighted Spin-Echo Scans (repetition time 3700 ms, echo time 92 ms, 256 × 256 matrix, 90° flip angle, 240 mm × 240 mm field of view, slice thickness 4 mm) in the same session. Voxel size was 0.9 × 0.9 × 4.00 mm.

Data analysis

Behavioral data (i.e. accuracy and response time) were analyzed using a 2 (level of detail of change) × 2 (speed of presentation) repeated measures design.

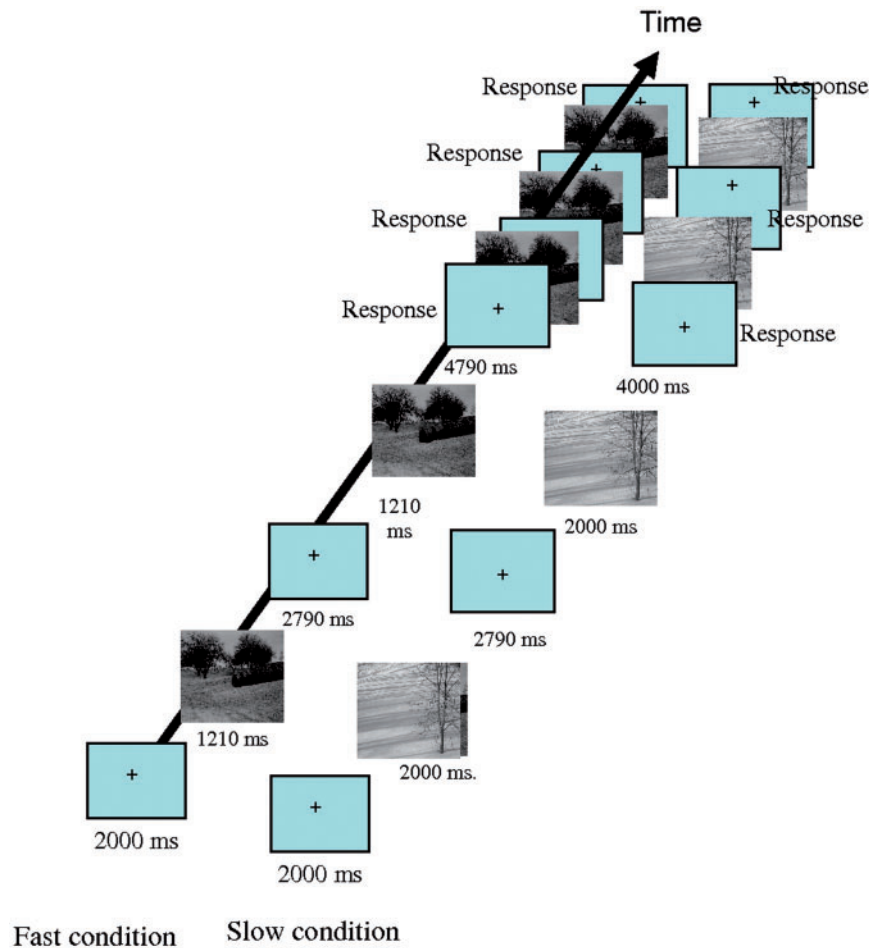


Fig. 2 Schematic of the change detection task. The design included four conditions: quickly presented major changes, quickly presented minor changes, slowly presented major changes, and slowly presented minor changes. Each condition consisted of presentation of an original image, followed by three (slow presentation condition) or four (fast presentation condition) either changed or unchanged images.

fMRI data were processed using SPM2 (Statistical Parametric Mapping) software (Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). Anatomical images were transformed stereotactically for each subject using linear rigid transformations. Functional scans were corrected for head motion and then realigned with reference to the first functional file. They were then coregistered with in-plane anatomical images and normalized to a Montreal Neurological Institute template. Next, images were spatially smoothed using a 6-mm full-width-at half-maximum Gaussian filter. Statistical parametric maps were then computed, using a random effects model, on overall group contrasts of major minus minor, fast minus slow and the 2×2 interaction. In separate, standard between-subject general linear model regressions, HSP mean score and HSP residual (i.e. HSP mean score after partialling out neuroticism and introversion) were each used as predictors for each contrast.

Regions of interest (ROI) were defined as 10-mm spheres. The center of the spheres were based at the peak coordinates of activation clusters identified from the literature to be

relevant to visual attention and oculomotor processes as well as motion processing (Petersen *et al.*, 1985; Tootell *et al.*, 1995; Corbetta *et al.*, 1998). These consisted of the right midbrain tegmentum, left intralaminar thalamic nucleus, right pulvinar nucleus of the thalamus, right intraparietal sulcus (IPS), junction of the intraparietal/transverse occipital sulcus, middle temporal complex, right inferior parietal lobule, the right superior temporal gyrus and the right precentral sulcus (i.e. middle frontal gyrus).

RESULTS

Behavioral results

Accuracy and response time were analyzed for only 12 of the 16 participants. The remaining four were clear outliers on missing values (no response or response not recorded, because it was after the allotted time). The four excluded each had >20 missing values ($vs \leq 3$ for each of the others).

Participants were more accurate when images were presented slowly than quickly, $F(1,11) = 22.86$, $P = 0.001$. There was also a trend toward being more accurate at spotting major than minor changes, $F(1,11) = 3.83$, $P = 0.08$.

Finally, there was a significant interaction, $F(1,11)=5.38$, $P=0.04$. Participants were most accurate when major changes were presented slowly, least when minor changes were presented slowly. Regarding response time, participants were actually somewhat faster when images were presented slowly, $F(1,11)=4.99$, $P=0.05$, plus evidenced a trend toward being slightly faster at responding to major than minor changes, $F(1,11)=3.25$, $P=0.10$. There was no interaction. (See Supplementary Table 1 for mean accuracy and response time by condition.)

Regarding SPS (and SPS residuals controlling for N and I), there were no significant associations with accuracy for fast minus slow, major minus minor, or interactions. For response time, however, there was a significant correlation of SPS with the minor-minus-major difference. The higher a participant was on SPS, the longer time the participant spent before responding to minor changes (relative to time spent on major changes), $r=0.64$, $P=0.02$. For example, on average, subjects overall took about 60 ms longer for minor than major changes. However, for individuals low in SPS, there was almost no difference; but those high in SPS took 132 ms longer to respond to minor than major changes. (Figures calculated from overall regression equation at one s.d. below and one s.d. above the SPS mean.) For SPS residuals, the same strong association remained as a near-significant trend, $r=0.51$, $P=0.09$. There was also a trend for SPS to correlate with responding relatively more quickly on slow than on fast trials, $r=0.52$, $P=0.08$; for SPS residuals, $r=0.44$, $P=0.16$. There were no significant correlations with the interaction.

Overall Group-level Contrasts

Overall, group-level contrasts (i.e. not considering associations with individual differences in SPS) indicated significantly greater brain activation in several regions when viewing images with minor *vs* major changes. In this overall group analysis, there was greater activation in the right lingual gyrus and cuneus of the occipital lobe, as well as in the insula, in response to minor changes than in response to major changes in the visual scenes (see Supplementary Table 2). In the overall group analysis, there was also significantly greater brain activation for major *vs* minor change in a number of areas in the occipital and frontal lobes, as well as in the cerebellum. The most extensive brain activation in response to the major *vs* minor change contrast was in the sublobar areas of the insula, globus pallidus, thalamus and caudate (see Supplementary Table 3). Finally, in the overall group analysis, there was significantly more brain activation in the inferior occipital gyrus and the globus pallidus in response to slow *vs* fast presentation of visual scenes (see Supplementary Table 4). No other overall contrasts were significant. (Supplementary Figure 1 shows brain slices for selected coordinates.)

Table 1 MNI coordinates of brain regions showing significant activation after the regression of SPS on the contrast of minor less major changes in visual scenes

Cluster location	Hemisphere	BA	Cluster size (voxels)	MNI coordinates			<i>t</i> -value
				<i>x</i>	<i>y</i>	<i>z</i>	
Middle temporal gyrus	L	37	154	−54	−54	−2	5.88
				−56	−54	−4	5.66
Clastrum	R	33	33	34	−12	−12	7.2
Sub-gyral temporal lobe	R	37	38	48	−46	−12	6.05
Declive of cerebellum	R	26	26	28	−60	−30	5.26
				16	−64	−30	5.25

T—contrasts thresholded (uncorrected) at $P=0.001$. Activation at 25 or more voxels, $P<0.001$.

Imaging results for associations with individual differences in SPS and SPS residuals

Contrasts of minor greater than major change conditions had strong and significant associations with individual differences in SPS in brain areas in the temporal lobe, the claustrum and the cerebellum (see Table 1). Figure 3 shows brain slices for selected associations of mean SPS scores with brain activation contrasts.

As shown in Table 2, these associations remained strong and significant after controlling for neuroticism (N) and introversion (I) scores, with additional strong and significant associations in the left temporal lobe as well as in the left temporooccipital junction. Additional activation was observed bilaterally in the inferior parietal lobule/precuneus. (See Figure 4 for brain slice for selected coordinates.)

Note that all significant associations were checked for outliers and were positive, such that those high on SPS, compared to those low in SPS, showed greater activation in these regions during the minor change blocks than during the major change blocks. There were no negative associations that met our significance threshold ($P\leq 0.001$, cluster size ≥ 25 voxels) for SPS or SPS residuals with this contrast. Nor were there any positive or negative associations with the fast *vs* slow contrast or with the interaction of major/minor with fast/slow.

Region of interest results for associations with SPS and SPS residuals

Both not controlling and controlling for neuroticism and introversion, contrasts of minor greater than major change conditions had strong and significant associations with SPS scores in functional areas related to visual attention and oculomotor control. As seen in Table 3, there were strong and significant associations in the right hemisphere in the temporoparietal cortical junction (TPJ; inferior parietal lobule and superior temporal gyrus), the intraparietal sulcus (IPS; lying between the superior and inferior parietal lobes) and the middle frontal gyrus (i.e. precentral sulcus). No significant associations met our threshold of 25 or more

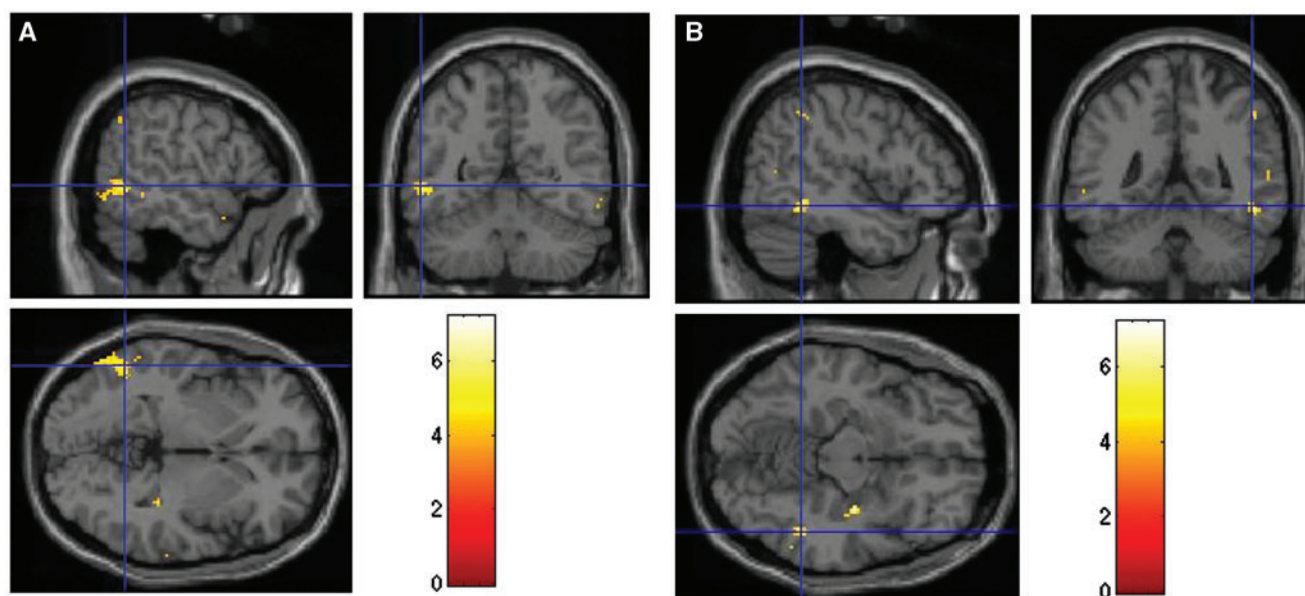


Fig. 3 BOLD in the left middle temporal gyrus and the right subgyral temporal lobe. Group average activation data for the association of HSP mean with the minor less the major change condition in the (A) left middle temporal lobe and the (B) right subgyral temporal lobe. Lighter color corresponds to greater activation. MNI co-ordinates for the center of the left (second peak) and right activation clusters were $-56, -54$ and -4 and $48, -46, -12$, respectively.

Table 2 MNI coordinates of brain regions showing significant activation after the regression of standardized SPS residual on the contrast of minor less major changes in visual scenes

Cluster location	Hemisphere	BA	Cluster size (voxels)	MNI coordinates			t-value
				x	y	z	
Clastrum	R		32	34	-12	-12	4.33
Occipital/temporal lobe							
Sub-gyral temporal lobe	R	37	58	48	-46	-12	4.40
Middle occipital gyrus	L	19	122	-56	-68	-8	4.21
Middle temporal gyrus	L	37		-52	-56	-6	4.02
Parietal lobe							
Precuneus	R	7	27	14	-60	48	4.15
Precuneus	L	7	25	-14	-58	50	4.61
Inferior parietal lobule	R	40	26	42	-50	52	4.93
Cerebellum							
Declive of posterior lobe	R			16	-64	-30	5.27
				28	-60	-30	4.92

T-contrasts thresholded (uncorrected) at $P = 0.001$. Activation for clusters of 25 or more voxels. $P < 0.001$.

voxels (false discovery rate of $P = 0.05$) in the middle temporal (MT/V5) area, the thalamic nuclei or the right tegmentum.

We report FDR thresholded data for the ROIs in Table 3 and not in Tables 1 and 2 (where we used an overall $P < 0.001$ with a 25 voxel minimum). This is because the results reported in Tables 1 and 2 derive from an exploratory analysis, whereas those reported in Table 3 are ROIs based

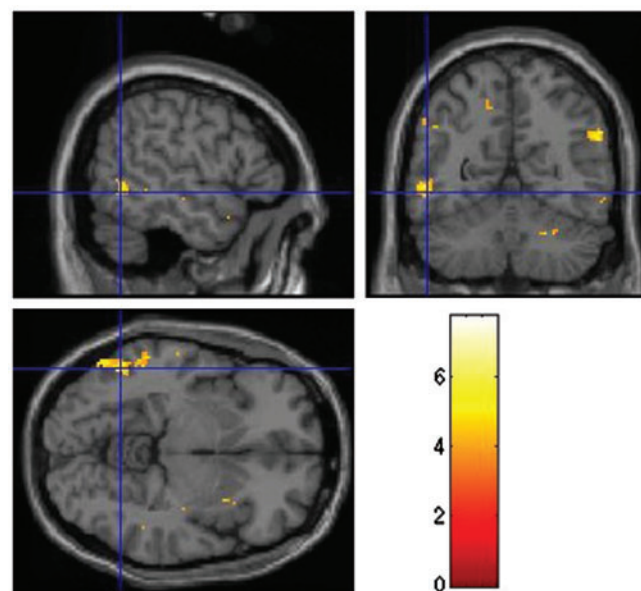


Fig. 4 BOLD in the left middle temporal gyrus. Group average activation data for the association of the standardized residual of the HSP mean and the minor less the major change. Lighter color corresponds to greater activation. MNI co-ordinates were $-52, -56, -6$.

on known functional areas of brain activation relevant to visual attention and oculomotor processes as well as motion processing (Petersen *et al.*, 1985; Tootell *et al.*, 1995).

DISCUSSION

Our study focused on the association of individual differences in the temperament/personality trait of SPS with

Table 3 MNI Coordinates for brain ROIs showing activation in response to correlation of SPS residual with minor less major changes in visual scenes

Cluster location	Hemisphere	BA	Cluster size (voxels)	MNI coordinates			t-value	
				x	y	z		
TPJ								
Supramarginal gyrus	R	40	60	56	−56	32	5.71	0.84
Inferior parietal lobule				54	−52	40	3.84	0.72
Superior temporal gyrus	R	22	185	62	−42	16	4.93	0.80
				58	−46	6	3.93	0.72
				66	−40	4	2.95	0.62
Intraparietal sulcus/TOS								
Superior occipital gyrus	R	19	155	34	−72	28	4.96	0.80
Precuneus				40	−74	38	3.33	0.66
SPL	R	7	130	26	−62	62	4.48	0.77
SPL				16	−66	62	2.83	0.60
Precuneus				12	−64	54	3.52	0.69
Inferior parietal lobule	R	40	355	42	−50	52	4.93	0.80
				40	−38	52	3.54	0.69
				34	−46	56	3.18	0.65
Middle frontal gyrus	R	6	380	28	2	54	3.77	0.71
				36	8	48	3.21	0.71
				42	6	56	2.88	0.61
Middle frontal gyrus	R	6	33	38	0	42	4.68	0.78
				38	10	48	3.33	0.66

FDR = 0.05. Activation at 25 or more voxels. TPJ, temporo-parietal cortical junction; SPL, superior parietal lobule; TOS, transverse occipital sulcus.

neural activation in a change detection task. Our results support a relationship between SPS and both increased response time and increased brain activation in relevant regions in response to subtle changes in stimuli. SPS is correlated with the minor-minus-major difference for both RT and activation in visual attentional areas. Conceptually, such results suggest that individuals high in SPS take longer to respond to minor changes in a scene and show more activation in visual attentional areas when responding to minor changes, because they are attending more closely to the subtle details of that scene.

There was a significant relationship between SPS and brain activation in the left middle temporal gyrus, the right claustrum, the right subgyral temporal lobe and the right declive of the cerebellum in response to minor vs major changes in stimuli. After controlling for the association of measures of neuroticism and introversion with SPS, this relationship remained significant. There was also activation in the bilateral inferior parietal lobe.

We interpreted the functionality of the activated brain areas based on previous fMRI studies with co-ordinates in approximately similar areas, as listed in the AMAT (http://www.dartmouth.edu/~antonia/AMAT_manual.pdf) neural coordinate database as well as literature searches of theoretically relevant brain functions.

Our findings from both whole-brain and region of interest analyses are in regions similar to those found in functional areas discussed in the visual processing literature, supporting the validity of the study. For example, we found strong and

significant brain activation in the claustrum when individuals high in SPS viewed minor differences in natural scenes. Although the function of the claustrum is unknown in humans, it has connections with the sensory and motor areas of the neocortex (Yamamoto *et al.*, 2007) and contributes to the processing of visual stimuli in the forebrain of the cat (Olson and Graybiel, 1980). Yamamoto and colleagues (2007) suggested that Lewy bodies found in the claustrum were related to visual misidentification, including visual hallucinations, which also implicates the claustrum in visual processing.

Our findings of associations of individual differences in SPS with activation in occipital and temporal regions and the precuneus relate to findings in the literature outlining various combinations of these areas as part of neural networks for object recognition (Kanwisher *et al.*, 1997) and for categorization and discrimination (Pernet *et al.*, 2004). Within these networks, the occipitotemporal junction (BA 19 and 37) is related to shape analysis (Kanwisher *et al.*, 1997), specifically to deviations in item shape (Piazza *et al.*, 2004).

SPS was also associated with activation in the declive of the vermis of the right cerebellum, an area implicated in oculomotor guidance. Previous research reports that the vermis codes eye position relative to the orbits, which is implicated in fixing the location of objects in space irrespective of changes in eye position (Law *et al.*, 1998). In a task such as ours, activation could be implicated in locating the original scene image in space and then remapping the scene on the changed image.

Individuals high in SPS evidenced greater brain activation in an additional network of functional brain areas that appear to be involved in visual attention and oculomotor processes [see review by Behrmann *et al.* (2004) and Small *et al.* (2003)]. Functional (i.e. IPS and TPJ) and anatomical (i.e. precentral sulcus) brain areas in our ROI analyses are implicated in the shifting of attention, both when individuals attend to peripheral visual stimuli and when they move their eyes and their attention to the same stimuli (Corbetta *et al.*, 1998, 2000). Participants in our study would have needed to attend to both overt and peripheral visual stimuli in order to detect changes in a visual scene. Our findings would also follow from the literature linking attentional processes to change detection (Rensink *et al.*, 1997). Since individuals high in SPS report an ability to notice subtle changes (Aron and Aron, 1997), it comes as no surprise that they have greater activation in attentional areas in response to a change detection task than do individuals low on the trait.

Although we found increased localized brain activation and response time differences linked to SPS, we did not find significant associations of SPS with accuracy. This may be due to low statistical power.

The finding that the basic pattern of results remains unchanged when controlling for measures of introversion and neuroticism is also important. It supports the idea that SPS makes a unique contribution to individual

differences in brain response, over and above major personality variables with which it has been found to be correlated in North American samples. This finding should be considered somewhat tentative, however, since there was little correlation between neuroticism and introversion or neuroticism and SPS in this sample. This may have been due to translation and reliability limitations of our measures of these personality variables or to the specificity of the relationship between SPS and neuroticism and introversion to a North American population.

The major limitations of our study are that it was exploratory and that the measures of the two questionnaire control variables may have been less than optimal. Another potential limitation was that we used a sample of convenience and not a sample selected on the basis of their SPS scores. The sample of convenience took advantage of an opportunity to include our task in an fMRI study being done for a different purpose. We realized that our study would require a substantial effect to be significant. However, given previous related research and the theoretical background of the SPS trait, we had some reason to expect that even with such a small, unselected sample, the effects might be large enough to be significant (as they were).

A strength of our study is that it is the first to investigate the neural correlates of SPS, adding to the growing literature with respect to this temperament/personality trait in adults. In addition, it begins to address the question of whether individuals high in SPS process sensory information more elaborately than individuals low in SPS, that is, with a greater attention to detail and with more attention to subtleties. Such 'more elaborate processing' is, we postulate, related to a greater degree of integration of various components of the neurological processes underlying visual processing.

The extent to which our results support that conclusion leads to a deeper understanding of the mechanisms through which SPS appears to influence a variety of important social and affective behavioral phenomena, including for example, the ways in which SPS creates greater vulnerability to poor parenting and other stressors leading to neuroticism and shyness (Aron *et al.*, 2005).

Potentially fruitful future research directions could include replication in a North American sample to examine generalizability of the results. It will also be important to examine potential alternative explanations for the self-reported sensitivity to subtleties of individuals high in SPS. In a review of the literature, Stelmack (1990) reports the enhanced sensory reactivity of introverts to punctate stimuli, as measured by electrodermal and electrocortical recordings. He attributes this reactivity to peripheral sensory processes. In a change detection task with natural scenes, such as ours, it is difficult to control changes in sensory thresholds while keeping all other variables constant. It will be important to try to administer some of the measures he reported (startle reflexes, event-related potentials and electrodermal activity) to investigate whether individuals high in SPS may have a

lower threshold for screening out sensory stimuli, alongside their ability to process stimuli more elaborately. Another important direction for future research is exploring the links of the visual and related brain regions identified here with areas directly implicated in the social and affective dimensions of SPS.

In conclusion, this research, the first neural investigation of SPS, lays a foundation for future studies of how cognitive and perceptual processes are affected by high levels of SPS. On a broader level, it could suggest that a greater understanding of personality might be gained by borrowing from the observation of biology that there are strategies behind 'personality differences' that involve a preference for pausing to process information more elaborately before acting.

SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

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