An electrophysiological insight into visual attention mechanisms underlying schizotypy

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Abstract

A theoretical framework has been put forward to understand attention deficits in schizophrenia (Luck SJ & Gold JM.. Biological Psychiatry. 2008; 64:34-39). We adopted this framework to evaluate any deficits in attentional processes in schizotypy. Sixteen low schizotypal (LoS) and 16 high schizotypal (HiS) individuals performed a novel paradigm combining a match-to-sample task, with inhibition of return (using spatially uninformative cues) and memory-guided efficient visual-search within one trial sequence. Behavioural measures and Event-related potentials (ERPs) were recorded. Behaviourally, HiS individuals exhibited a spatial cueing effect while LoS individuals showed the more typical inhibition of return effect. These results suggest HiS individuals have a relative deficit in rule selection – the endogenous control process involved in disengaging attention from the uninformative location cue. ERP results showed that the late-phase of N2pc evoked by the target stimulus had greater peak latency and amplitude in HiS individuals. This suggests a relative deficit in the implementation of selection – the process of focusing attention onto target features that enhances relevant/suppresses irrelevant inputs. This is a different conclusion than when the same theoretical framework is applied to schizophrenia, which argues little or no deficit in implementation of selection amongst patients. Also, HiS individuals exhibited earlier onset and greater amplitude of the mismatch-triggered negativity component. In summary, our results indicate deficits of both control and implementation of selection in HiS individuals.

Keywords: Schizotypal personality traits; ERP; N2pc; Mismatch-triggered negativity; Executive control

1. Introduction

The fully-dimensional approach to the relationship between schizotypal personality traits and schizophrenia (SZ) describes schizotypy as a continuum throughout the general population ranging from low schizotypy (LoS) and psychological health to high schizotypy (HiS) and proneness to developing psychosis (Claridge and Beech, 1995; Nelson et al., 2013). A recent review of neurobiological, neuropsychological, social and environmental evidence supports the idea that schizotypy in healthy populations is fundamentally linked to disorders on the SZ spectrum (Nelson et al., 2013). Specifically, research has consistently reported cognitive deficits common to HiS individuals and SZ spectrum disorders including: executive functions, attention, working memory and prepulse inhibition dysfunctions (Giakoumaki, 2012). A recent study from our lab (Fuggetta et al., 2014) aimed to evaluate quantitative electroencephalographic (qEEG) measures of power spectra as potential biomarkers of the proneness towards the development of psychosis in exactly the same individuals who participated in the current investigation. With the application of a “resting-state” experimental design, where oscillatory brain dynamics under three minutes of eyes-closed condition were assessed, it was found that HiS individuals exhibited an increase of amplitude (i.e. synchronisation) in low-alpha band cortical oscillations, which suggested unusual high-level attention (Fuggetta et al., 2014). The current study aimed to further understand which attentional processes underlie deficits among individuals with high psychosis-proneness using both behavioural and electrophysiological approaches. It is important to examine cognitive deficits in schizotypal individuals because cognitive deficits often predict functional outcome in psychiatric disorders such as SZ (Green et al., 2004). Identifiable attentional deficits in HiS individuals among the general population could serve as risk factors of developing psychosis.

Attention is a complex cognitive construct that can be defined in many ways, making precise descriptions of attention deficits in SZ difficult (Luck et al., 2006). Luck and Gold (2008) presented a framework designed to elucidate the pattern of attention impairments found in SZ patients under a variety of paradigms (Luck and Gold, 2008). Here we adopted Luck and Gold's (2008) framework to interpret the results of our study and define the specific deficits in the attention processes of HiS individuals. Luck and Gold's framework subdivides the broad construct of attention into 'rule selection' and 'input selection' to help understand participants' performance (Luck and Gold, 2008). Attention is sometimes used to select between multiple competing rules. Rule selection is important when suppressing a rule previously learned or automatically associated with a particular stimulus. The Stroop task is an example of a 'rule-selection task' in which executive control must override a prepotent response. When asked to name the ink colour, the individual must suppress the prepotent rule to read the word, and the cost is seen as increased reaction times (RTs).

Attention can also select between multiple sensory inputs competing for access to further processing. Such 'input selection' is important when the desired input lacks sufficient bottom-up salience to win the competition for further processing. Spatial cuing and visual search paradigms are most commonly used to examine input selection. For example, in spatial cueing, a salient cue, automatically captures attention to its location. This biases competition among subsequent stimuli (e.g. a target stimulus is more easily identified at a cued vs. an uncued location). Input selection is subdivided into 'control of selection' — referring to the processes that guide attention to task-relevant inputs and 'implementation of selection' — referring to the processes that enhance the processing of the relevant inputs and suppress the irrelevant inputs (Luck and Gold, 2008).

These constructs are closely tied to both working memory (WM) and executive systems. Both systems have strong but indirect influences on control and on implementation of input selection. For example a stimulus template held in WM may be used by selection control processes to direct attention to matching target stimuli. Executive functions implementing task rules may be used by implementation of selection processes to enhance the task-relevant features of the targets. Control of selection processes typically involves the prefrontal and parietal cortices, while implementation of selection typically occurs within the visual cortex (Luck and Gold, 2008).

Luck and Gold (2008) suggests that SZ involves a deficit in the control of selection but not in the implementation of selection; however, prior electrophysiological research supporting this view is scarce (Luck et al., 2006). Further, there are few studies of high schizotypal individuals which bear on this framework. Evidence does suggest that HiS individuals likewise show impaired rule selection. A study by Larrison, Ferrante, Brand & Sereno (2000) found evidence of deficits in voluntary control of attention in individual prone to develop psychosis. HiS made more errors than LoS in a task requiring a saccade away from a lateralised target. This can be interpreted as difficulty in control of selection insofar as the HiS group had difficulty suppressing a prepotent response when required to direct overt attention to a laterally opposite location. Other evidence that HiS have difficulty in selecting appropriate information or in suppressing a response was found by Cimino & Haywood (2008) using a Stroop task in which the required response switched periodically between stating the word or its colour.

In this study, we aimed to examine the control and implementation of input selection and rule selection processes in HiS and LoS individuals to investigate whether HiS individuals show relative deficits in these processes similar to SZ patients. Thus we adopted

both behavioural and electrophysiological measures in a single experiment designed to assess different processes of attention. In particular we used a delayed match-to-sample task in which participants were shown a shape cue (S1) followed by a task-irrelevant and uninformative spatial cue, followed by a search array (S2) containing a target shape among homogeneous distractors. Participants had to identify whether the target shape in S2 was the same (match) or different (mismatch) from S1. Thus a single experiment combines a delayed match-to-sample task (Wang et al., 2004; Wang et al., 2003a) with a variant of spatial cueing (Posner et al., 1985) and efficient visual search paradigms (Treisman and Gelade, 1980) within one trial sequence. This experimental approach allows us to examine several aspects of attention, executive function and short-term visual memory (STVM).

1.1 Inhibition of return paradigm

Human perceptual systems have evolved mechanisms of internally mediated shifts of attention (i.e. covert orienting) to select important information, while ignoring uninformative information (Mushquash et al., 2012). When a visual event is not task-relevant and attention has had time to disengage from it, an inhibitory aftereffect can be measured in delayed responding to stimuli subsequently displayed at the originally cued location. This is called inhibition of return (IOR; Klein, 2000).

Using an IOR paradigm, Klein provided preliminary evidence that SZ patients are slower in voluntary (i.e. endogenous) disengagement of attention from a cued location prior to the appearance of a target (Klein, 2005). Other IOR studies suggest even more severe abnormalities in voluntary attentional control (Gouzoulis-Mayfrank et al., 2006; Gouzoulis-Mayfrank et al., 2004; Kebir et al., 2010). Using a meta-analytic approach, Mushquash et al., (2012) have shown that the Stimulus Onset Asynchrony (SOA) where facilitation (i.e. spatial cueing) gives way to IOR is abnormally long in SZ patients compared with controls (758 ms

vs. 293 ms, respectively). This fits with the idea that SZ patients have a deficit in rule selection (Luck and Gold, 2008).

We incorporated an IOR paradigm to examine the rule selection in HiS. A task-irrelevant and uninformative peripheral spatial cue was presented before the peripheral target (S2). The cued location did not predict the target location as it was invalid on the majority of trials (75% invalid trials). Therefore, participants must inhibit the prepotent rule to maintain attention on the spatial cue and instead select a task-appropriate rule: shift attention back to the central fixation and await the appearance of the target. Luck & Gold (2008) cite Maruff et al. (1996) as an example of impairment of rule selection on a task similar to ours. Participants were shown a peripheral cue indicating a target would appear at an opposite, uncued location. The cue automatically captures attention and thus is an example of a prepotent rule to attend to the sudden onset of the stimulus. Participants had to suppress this rule and select the task-relevant rule, to direct their attention to the uncued location. SZ patients exhibited longer reaction times in this task, which can be interpreted as impairment of control of rule selection (Luck and Gold, 2008). It is a fairly standard finding that SZ patients show poorer performance on rule selection tasks and can be well-described as impairment in executive control over rule selection (Luck and Gold, 2008). We tested whether this is also the case for HiS individuals.

1.2 Visual search paradigm

In this study, participants located a pop-out colour target in an array of homogeneous distractors in S2 and indicated whether the target shape was the same (matching) or different (mismatching) as the cue in S1. To assess control and implementation of input selection, we examined the ERP N2pc component. This occurs between ~200 and 300 ms post-target array, and manifests itself as an enhanced negativity at posterior electrodes contralateral to the

target. It is commonly employed as a marker for the focus of spatially selective attention during visual search tasks (Eimer, 1996; Kiss et al., 2008; Luck and Hillyard, 1994a; Luck and Hillyard, 1994b; Mazza et al., 2009; Woodman and Luck, 1999; Woodman and Luck, 2003). Hopf et al. (2000) using Magnetoencephalography (MEG) and source localisation procedures, revealed that the N2pc is composed of two distinct subcomponents: an early phase (180–220 ms) originating in the parietal cortex and a late phase (220–240 ms) originating in the infero-temporal visual areas. However, a later study has not replicated the parietal source (Hopf et al., 2006). In terms of functional significance, the early phase of the N2pc seems to be related with the control of input selection; the processes involved in the initiation of attention shifts to a task-relevant item (Hopf et al., 2000; Corbetta et al., 1995). Fuggetta et al. (2006) with a combined transcranial magnetic stimulation (TMS) and ERP study have demonstrated that a single pulse of TMS delivered over the right posterior parietal cortex at 100 ms after the target array onset creates an impairment of search performance in terms of RTs; moreover the RT impairment correlated with TMS induced suppression of the early parietal subcomponent of N2pc. These results provide further evidence for the functional role of the parietal circuitry in the process of initiating attention shifts in the direction of task-relevant inputs (Fuggetta et al., 2006). The late phase of N2pc seems to be related with the implementation of input selection (Hopf et al., 2000; Heinze et al., 1994; Luck & Hillyard, 1994b) as it is eliminated when distractors are absent and its amplitude increases with the number of distractors. These observations suggest that it may reflect the filtering of distractor items (Luck et al., 1997b).

Research examining N2pc onset time has shown that SZ patients can shift their attention to a target at the same rate as control subjects and no effect of SZ on N2pc amplitude or peak latency, even though the RTs of the SZ group were delayed by over 100 ms (Luck et al., 2006). Thus it has been suggested that implementation of selection

processes reflected by the N2pc component appears to be unimpaired in SZ, both in terms of the time required to shift attention and the amount of attention that can be allocated (Luck et al., 2006; Luck and Gold, 2008). However, Luck et al. (2006) used a measure of N2pc obtained from across the entire duration of the component. Given that the early and late phases are assumed to relate to different processes, it could be the case that considering the early and late phases separately would give a clearer picture of any deficits in the control and implementation of selection in HiS individuals. We examined the two separately in this study.

1.3 Match-to-sample paradigm

When we repeatedly encounter an object we become faster and more accurate at identifying it. This effect has received a great deal of interest because it is one of the most basic forms of memory, influencing the perception and interpretation of the world (Henson, 2003; Buckner et al., 1998; Schacter and Buckner, 1998). ERP studies have shown that delayed match-to-sample tasks elicit a larger bilateral N2 component (also called N270 or ‘mismatch-triggered negativity’ Bennett et al., 2014) on trials in which the features between cue (S1) and target (S2) differ (‘mismatch trials’). A simple delayed match-to-sample task using shape stimuli known to evoke the mismatch-triggered negativity component was shown with functional magnetic resonance imaging (fMRI) to result in increased activity in the right anterior cingulate cortex (ACC) and also in the right dorsolateral prefrontal cortex (DLPFC) (Zhang et al., 2008). This mismatch-triggered negativity, distinct from the N2pc component discussed above, typically peaks in anterior electrode sites around 270 ms and can be elicited by mismatches in various feature dimensions (Cui et al., 2000; Zhang et al., 2005; Zhang et al., 2001; Mao and Wang, 2007; Yang and Wang, 2002; Zhang et al., 2001; Wang et al., 2002; Wang et al., 2000; see Folstein and Van Petten, 2008, for a review on N2 effects).

Further, when participants process multiple sources of feature mismatch, such as shape and colour, the negativity is observed all over the scalp, but is more pronounced at fronto-central regions and prolonged up to around 500 ms (Chen et al., 2006; Mao and Wang, 2007; Wang et al., 2004; Wang et al., 2003a; Wang et al., 2003b).

Collectively, these results suggest that mismatch-triggered negativity is a robust effect which represents endogenous mismatch between an STVM representation of a shape cue stimulus (S1) and a second mismatching target stimulus (S2). Recently we have found that the addition of homogeneous distractors, delays the mismatch-triggered negativity by purely attentional means, probably postponing when the S1-S2 matching process itself occurs. This affects mismatch judgments more than match judgments, reflecting the increased difficulty of the former (Bennett et al., 2014). Therefore, including match and mismatch conditions in an array of homogenous distractors in the present study allows us to look for relative deficits under a lower and a higher level of attentional demand.

To our knowledge, previous research has not assessed mismatch-triggered negativity during a delayed match-to-sample task in HiS individuals. The task allows us to examine participants' ability to compare a target stimulus to a representation in WM by assessing amplitude of mismatch-triggered negativity. Thus performance on this task depends on the effective use of WM and executive function. We expected to find greater mismatch-triggered negativity along with increased RTs in mismatch trials in individuals with high psychosis-proneness.

We used indirect behavioural and direct electrophysiological measures to examine potential relative deficits in attention mechanism in HiS compared with LoS individuals. We examined rule selection, control of selection and implementation of input selection as defined in Luck and Gold's (2008) conceptual framework for attention processes. We also attempted

to establish whether any such relative deficits indicated by N2pc and mismatch-triggered negativity components, may be able to detect individuals from the general population with a high-risk of developing psychosis by correlating ERP measures with schizotypal trait scores. The analysis of similarities and differences in the mechanism of visual attention system between HiS and SZ patients is of relevance to further evaluate the fully dimensional approach of the relationship between schizotypal personality traits and SZ (Nelson et al., 2013).

2. Method

This study was approved by the local ethical committee of the University of Leicester's School of Psychology, in accordance with the Declaration of Helsinki. All participants gave written informed consent and received course credit for participating. Participants were fully debriefed about the purpose of the study.

2.1 Participants

An initial group of 165 (140 females, 18–26 years) undergraduate psychology students from the University of Leicester (UK) completed the Oxford–Liverpool Inventory of Feelings and Experiences (O-LIFE) questionnaire (Mason and Claridge, 2006; Mason et al., 1995). Participants whose scores on either the ‘Unusual Experiences’ or ‘Cognitive Disorganization’ subscale of the O-LIFE were below the inter-quartile range of normative data for their age and gender (Mason and Claridge, 2006), were classified as LoS individuals ($N = 19$). Those scoring above were classified as HiS ($N = 19$). These 38 individuals were selected to participate in the experimental part of the study. Of these, data from six participants were excluded due to excessive EEG artifacts. In particular, participants were excluded for further

ERP analyses if the number of segments kept after artefact-rejection procedure were exceeding two standard deviations from the mean of the whole group (merging HiS and LoS participants). This selection criterion led to the exclusion of three HiS individuals and three LoS individuals. Therefore, ERP data from 16 LoS (18–22 years) and 16 HiS participants (18–25 years) were analysed. Subject characteristics for both groups are detailed in Table 1. All participants reported no use of medication, history of chemical dependency or neurological, psychiatric/psychological disorders or closed head injuries. The two groups did not differ in terms of age, gender and handedness. The HiS group exhibited higher mean scores than the LoS group on all the four subscales of the O–LIFE questionnaire.

< Table 1 about here >

2.2 Self-report measure of psychosis-proneness

The O–LIFE (Mason and Claridge, 2006; Mason et al., 1995) is a four-scale self-report measure of 104 items selected on the basis of factor-analytic studies of scales that have been employed in the past to assess psychotic-like features in the general population. The reliability and validity of its items have been established (Mason and Claridge, 2006). Its items show high internal consistency (all alphas between 0.77 and 0.89; Mason et al., 1995), and good test–retest reliability (0.70; Burch et al., 1988). The construct validity of the scale as a measure of schizotypy has been established in studies across many fields of interest (see Mason and Claridge, 2006 for review). The questionnaire assesses the following four dimensions: ‘*Unusual Experiences*’ reflects the positive aspects of psychosis, and consists of items assessing hallucinatory experiences, unusual perceptual aberrations, and magical thinking. ‘*Cognitive Disorganization*’ consists of items assessing difficulties with decision making and concentration, as well as social anxiety; it reflects the disorganised aspect of psychosis. ‘*Introvertive Anhedonia*’ contains items assessing the deficiency of gratification

which derives from social contact, physical activities, combined with aversion to physical and emotional intimacy. It reflects the negative aspects of psychosis. '*Impulsive Non-conformity*' consists of items assessing impulsive, aggressive, and anti-social behaviour.

2.3 Procedure

Participants were naïve to the purpose of the investigation. All were tested individually and were presented with instructions to complete the O-LIFE questionnaire in conventional paper-and-pencil form. At a later date, 38 participants underwent the experimental stage. The experiment lasted for approximately 60 min.

2.4 Stimuli and task

Stimuli were presented on a 21" monitor (ViewSonic G810) (40 cm horizontal $\times$ 30 cm vertical) with a refresh rate of 100 Hz and a resolution of 1024×768 pixels. The monitor was located in a black viewing tunnel so that only the display was visible. The participant's head was stabilised in a head and chin rest. Viewing distance was 57 cm. The monitor continuously displayed a white 0.4° fixation spot in the centre of a grey 26° diameter circle, shown against a black background. Four 2.1° empty white circles were present 10° peripherally in the top-left, top-right, bottom-left and bottom-right quadrants. This limited visual search to the four positions needed to assess cue-target position conflict across horizontal and vertical hemifields. A trial consisted of the following sequence of events, shown in Fig. 1: A) shape cue, B) fixation, C) non-predictive position cue, D) delay, E) target array, and F) response time.

< Figure 1 about here >

The foveally presented shape cue (S1) was either a 2° hexagon (50% of trials) or diamond (50% of trials) and either red (50% of trials) or green (50% of trials) (A). This was followed by a fixation period (B). Next, a position cue – a 2° white star – appeared within one empty white circle (on 80% of trials) or simultaneously in all four circles (on 20% of trials). After a delay (D) following cue offset, the target array (S2) was presented for 150 ms (E). The target was either a hexagon (50% of trials) or diamond (50% of trials) and always of the same colour as the shape cue (randomised from trial to trial). The shape cue and target matched on 50% of trials and mismatched on the other 50%. The target appeared within one of the four empty white circles among fifteen homogeneous distractors — 2° filled circles. Visual stimuli were spaced evenly on the circumference of an imaginary 10° radius circle around the central fixation point, as shown in Fig. 1. The distractors were always of a different colour from the target and all either red or green (i.e. either ‘red target, green distractors’ or vice versa). Thus the dimensions of the pop-out search were both a colour search and a shape search.

The participants' task was to indicate via a response box whether the target shape (S2) matched or mismatched the shape cue (S1). The position cue did not predict the location of the target stimuli, and no instructions were given to the subjects regarding spatial cue-target contingencies. The centre of the response box was aligned with the participants' midline. The two types of response were made with the left and right index fingers. The mapping was counterbalanced across subjects. Speed and accuracy were encouraged. RT and correct/incorrect response data were recorded. Participants received auditory feedback — a 200 ms low vs. high pitch ‘beep’ sound, regarding accuracy. Participants were instructed to maintain central fixation and to blink only after a response had been made after the “beep sound”. Before the main experiment, participants completed 24 practice trials to familiarise themselves with the task and adjust to the requirements.

Participants completed 640 trials in eight blocks of 80 trials. Participants were allowed to pause between blocks. Each block consisted of 80 pseudo-randomly distributed trials from each of the match vs. mismatch conditions. The position cue-target SOA (700 vs. 1200 ms) was randomised within blocks. In particular, the position-cue was either at the same location as the target (valid trials), in an adjacent quadrant above/below the target (invalid trials with vertical deviation), in an adjacent quadrant to the left/right (invalid trials with horizontal deviation), in the opposite quadrant (invalid trials with both vertical and horizontal deviations) or in all four locations (neutral trials). Thus single-position cue trials made up 80% of the total trials and only 25% of these were valid trials. Trials were pseudo-randomly selected to maintain this proportion within each block.

2.5 EEG data acquisition

Continuous EEG signals were recorded by a DC 32-channel amplifier (1-kHz sampling rate, 250 Hz high cut-off frequency; Brain Products Inc., Germany). The EEG activity was recorded from unshielded and sintered Ag–AgCl electrodes via a Waveguard elastic cap (CAP-ANTWG64; ANT, Netherlands) using a subset of the international 10–5 electrode system sites (Fp2, F3, Fz, F4, FC5, FC1, FC2, FC6, C3, Cz, C4, CP5, CP1, CP2, CP6, P3, Pz, P4, PO7, PO3, PO4, PO8, O1, Oz, and O2). The right-earlobe electrode served as an on-line reference. EEG waveforms were re-referenced off-line to the average of the right and left-earlobe electrodes (Luck, 2005). Two electrodes placed in a bipolar montage at approximately 1 cm from the outer canthi of both eyes served to record the horizontal electrooculogram (HEOG). The vertical electrooculogram (VEOG) and blinks were recorded and detected from one electrode positioned below the right eye and Fp2 and referenced to the right earlobe. Electrode impedance was kept below 5 k Ω .

2.6 EEG analyses

EEGs were epoched from 200 ms prior to target search array onset to 600 ms after, giving a total epoch of 800 ms. Each EEG epoch was visually inspected off-line, and those with ocular artefacts (as indicated by HEOG activity exceeding $\pm 40 \mu\text{V}$ and VEOG activity exceeding $\pm 80 \mu\text{V}$) were excluded (26% rejection rate for LoS; 20% for HiS. In both groups, this left about 50 trials for each of the 10 conditions, including 5 levels of cue-target location $\times$ 2 levels of SOA).

Separate average ERPs were computed for six regions of interest (ROI) each consisting of a group of electrodes: F3, FC1 and FC5 = 'Left fronto-central region' (FCL); F4, FC2 and FC6 = 'Right fronto-central region' (FCR); C3, CP5 and CP1 = 'Left centro-parietal region' (CPL); C4, CP6 and CP2 = 'Right centro-parietal region' (CPR); P3, PO3, PO7 and O1 = 'Left parieto-occipital region' (POL); and P4, PO4, PO8 and O2 = 'Right parieto-occipital region' (POR). ERPs were computed for trials relative to a 200 ms pre-stimulus baseline. ERPs were then filtered using 0.5 Hz high-pass, 45 Hz low-pass, and 50 Hz notch filters.

To isolate the magnitude of the N2pc component elicited by the target search array, at lateral occipital PO7/PO8 electrodes and POL/POR sites pairs, we computed difference waves by subtracting ipsilateral from contralateral electrodes relative to the target location. To eliminate any hemispheric asymmetries that were unrelated to attention, we averaged the difference waves across left- and right-hemisphere PO7/PO8 electrodes and POL/POR site pairs (see Luck et al., 2006). The onset of the N2pc was defined as the time at which posterior-lateralised ERPs first differed using a "neuron-anti-neuron" approach (Purcell et al., 2013) (see below). The mean N2pc difference wave amplitude was measured during two 40 ms non-overlapping time periods: between 191 and 231 ms and between 232 and 272 ms

N2pc peak latency defined as the local peak latency of the difference waves between 191 and 300 ms (Luck, 2005).

The mismatch-triggered negativity component is a bilateral ERP component sensitive to perceptual mismatch between an initial stimulus S1 (shape cue) and a subsequently presented second stimulus S2 (target shape) (Wang et al., 2004; Bennett et al., 2014). To isolate the magnitude of the mismatch-triggered negativity component elicited by the target search array, we computed difference waves by subtracting match from mismatch trials. The onset of the mismatch-triggered negativity component was defined by the neuron-anti-neuron” approach applied to the average of all six ROIs. The mean mismatch-triggered negativity wave amplitude was measured during a 200 time period between 344 and 544 ms.

2.7 Statistical analysis

In all ANOVAs, Greenhouse–Geisser epsilon adjustments for non-sphericity were applied where appropriate. Post hoc paired *t*-tests were Bonferroni corrected for multiple comparisons. For all statistical tests, $p < .05$ was considered significant. Preliminary statistical analyses did not reveal any significant main or interaction effects of SOA in either the ERP or behavioural data so we collapsed across SOA levels for all analyses reported here.

2.7.1 Behavioural data

For each participant, only data for trials with correct responses and RTs between 150 and 2000 ms, and also with values within three standard deviations from the individual's mean RT were analysed. RT and error rate data were analysed with two mixed analyses of variances (ANOVAs). Each ANOVA had a between-subjects factor: ‘Group’ (HiS vs. LoS) and two within-subjects factors: ‘Trial Type’ (match vs. mismatch trials), and ‘Cue-Target

Location' (same quadrant vs. adjacent quadrant above/below vs. adjacent quadrant left/right vs. opposite quadrant vs. all four locations cued).

To assess the relation of valid trials to the four other position cue-target combinations, RT data were submitted to four separate mixed ANOVAs. All four ANOVAs contained a between-subjects factor: 'Group' (HiS vs. LoS). The four ANOVAs were distinguished by their within-subjects factor with two levels: 'Cue-Target Location' which was either 1) same quadrant vs. adjacent quadrant above/below, 2) same quadrant vs. adjacent quadrant left/right, 3) same quadrant vs. opposite quadrant or 4) same quadrant vs. all four locations cued. In the case of significant 'Group' by 'Cue-Target Location' interactions, a post-hoc *t*-test was repeated using difference values (uncued RT – cued RT) to examine the attentional effects of the cues.

2.7.2 ERP data

The onset of the N2pc component, which indicates selection time, was defined using the “neuron-anti-neuron” approach (Purcell et al., 2013). Specifically, for every millisecond, a *t*-test (2-tailed) was conducted comparing the contralateral and ipsilateral waveforms from posterior ROIs (POL/R). Selection time in our study was defined as the first time point reaching a conservative $p < 0.01$ (2-tailed) preceded by at least 5 consecutive milliseconds at $p < 0.05$ (2-tailed) and which was followed by 30 subsequent milliseconds reaching $p < 0.001$ (2-tailed), to eliminate false alarms. These criteria are similar to previous reports on the origin of the macaque N2pc human homologue (Monosov et al., 2008; Purcell et al., 2013). This procedure was also used to define the onset of latency of the mismatch-triggered negativity component, averaged across FCL/R, CPL/R, POL/R ROIs, using the difference between match and mismatch trials. We estimated the onset latency of the N2pc component (i.e. selection time) and the mismatch-triggered negativity component across the entire group of

participants and also did this separately for the HiS and LoS groups. To test for any significant differences in the onset latency of both N2pc and mismatch-triggered negativity components, ERP data were submitted to two separate mixed ANOVAs. Both ANOVAs contained a between-subjects factor: 'Group' (HiS vs. LoS) and a within-subjects factor with three levels: 'Time point' (baseline before the onset of the component vs. selection time for HiS vs. selection time for LoS).

The N2pc magnitude was analysed with a mixed ANOVA with a between-subjects factor: 'Group' (HiS vs. LoS) and two within-subjects factors: 'Time period' (191–231 vs. 232–272 ms), and 'Cue-Target Location' (same quadrant vs. adjacent quadrant above/below vs. adjacent quadrant left/right vs. opposite quadrant vs. all four locations cued). The beginning of the first time period coincided with the onset of N2pc (i.e. selection time), which was 191 ms post-target array onset (see results section). The mismatch-triggered negativity component magnitude was analysed with a mixed ANOVA with a between-subjects factor: 'Group' (HiS vs. LoS) and three within-subjects factors: 'Sagittal Axis' (fronto-central vs. centro-parietal vs. parieto-occipital ROI), 'Hemisphere' (left vs. right ROI), and 'Cue-Target Location' (same quadrant vs. adjacent quadrant above/below vs. adjacent quadrant left/right vs. opposite quadrant vs. all four locations cued). The beginning of the 200 ms time period analysed coincided with the onset of mismatch-triggered negativity which was 344 ms (see results section).

7.2.3 Correlations between Schizotypy personality traits and ERPs measures

Pearson's product-moment correlations were conducted to investigate the relationship between scores on the sub-scales of the O-LIFE questionnaire and ERP measures. Correlation coefficients were computed in the whole sample, merging His and Los individuals and separate for each of the two groups of participants. If more than one electrophysiological

index of attentional processes were significantly associated with the scores in one of the sub-scales of the multidimensional measure of schizotypal traits then a separate hierarchical multiple linear regressions was conducted. This statistical analyses was implemented to test both the unique predictive capacity of each ERP measure and their cumulative effect of an increase in the predictability of Schizotypy personality sub-scales scores if used in combination. The dependent variable for the regression analyses was the score from one of the four sub-scales of O-LIFE questionnaire. Whereas those ERP measures that significantly correlated with the sub-scale were entered as independent predictor variables. Fisher's r -to- z transformation test (Fisher, 1921) was used to assess the significance of the differences in correlation coefficients found in the two groups of HiS and LoS individuals. An SPSS syntax (<http://imaging.mrc-cbu.cam.ac.uk/statswiki/FAQ/WilliamsSPSS/Fisher>) has been used for this purpose.

3. Results

3.1 Behavioural results

Mean error rate ($\pm$ SE) was $15.1 \pm 2.0\%$ in the LoS group and $15.5 \pm 2.0\%$ in the HiS group. There was a significant main effect of Trial Type $F_{(1, 30)} = 16.58, p < .001, \eta p^2 = .36$. Post-hoc pairwise comparisons revealed that accuracy was significantly reduced in mismatch compared to match trials in both LoS and HiS groups ($p < .01$ and $p < .05$, respectively). No other main effects or interactions were significant.

Mean RT ($\pm$ SE) was 722 ± 25 ms in the LoS group and 725 ± 25 ms in the HiS group. There was a significant main effect of Trial Type $F_{(1, 30)} = 58.38, p < .001, \eta p^2 = .66$. Post-hoc pairwise comparisons revealed that RTs were significantly increased in mismatch compared to match trials in both LoS and HiS groups ($p < 0.001$). No other main effects or interactions were significant.

Overall, participants were 58 ms faster and 5.9% more accurate in match trials compared to mismatch trials, indicating improved behavioural performance in match trials. The behavioural results for the two groups of participants were extremely similar. Supplementary Figure S1 shows the groups' behavioural performance in terms of mean RTs and error rates.

< Inline Supplementary Figure S1 about here >

Of the ANOVAs performed to assess the relation of valid trials to the four other cue–target combinations, only the one comparing valid trials vs. cue–target appear in adjacent quadrants above/below each other distinguished between the two groups. There was a significant Group $\times$ Cue–Target Location interaction, $F_{(1, 30)} = 6.88$, $p < .05$, $\eta p^2 = .19$. The post-hoc t -test using RT difference values (adjacent quadrants above/below – same quadrant) revealed that HiS individuals showed facilitation/spatial cueing (+9.7 ms) whereas LoS individuals showed IOR (–11.0 ms). Overall the significant difference between both groups with $t_{(30)} = 2.62$, $p < .05$, was 20.7 ± 7.9 ms. Fig. 2 shows the groups' behavioural performance in terms of RT difference scores.

< Figure 2 about here >

3.2 ERP results

3.2.1 N2pc

The N2pc results from PO7/8 electrodes and POL/R ROIs were extremely similar, thus only the POL/R ROI results are reported. Grand average ERP waveforms for POL/R ROIs are shown in Fig. 3 whereas ERP waveforms for PO7/8 electrodes are shown in Supplementary Figure S2.

< Figure 3 about here > < Inline Supplementary Figure S2 about here >

Fig. 3A–B shows separate contralateral and ipsilateral waveforms for contralateral and ipsilateral targets relative to the hemisphere of the recording ROI. For both the HiS and LoS groups, the N2pc component can be seen as a more negative (i.e. less positive) contralateral voltage beginning at approximately 200 ms post-stimulus during visual search. N2pc onset latency (i.e. selection time) was measured from these waveforms. The time periods chosen for analyses are indicated with grey vertical lines, with the N2pc onset latency indicated by the first line.

Across all participants, the N2pc onset (i.e. selection time) was 191 ms with $t_{(31)} = -2.96$, $p < .01$ (note that the increased amount of participants leads to increased statistical power, resulting in an earlier detection of a significant difference i.e. onset time). For HiS individuals the selection time was 197 ms with $t_{(15)} = -3.00$, $p < .01$ and for LoS individuals it was 196 ms with $t_{(15)} = -2.99$, $p < .01$. The ANOVA conducted to test the difference in N2pc onset of HiS against that of LoS revealed that Group $\times$ Time point interaction was non-significant $F_{(2, 60)} = 0.03$, $p = \text{ns}$, $\eta p^2 = .00$. These results demonstrate that the time required for the initial shift of attention to be reliably focused on the target (Purcell et al., 2013), was identical for the HiS and LoS groups.

The N2pc appears substantially larger and prolonged in the HiS group. These observations were substantiated by statistical analyses. There was a significant interaction between Group $\times$ Time period and Contralaterality with $F_{(1, 30)} = 6.52$, $p < .05$, $\eta p^2 = .18$. Post-hoc pairwise comparisons revealed that in the case of early N2pc time-period (191–231 ms), the lateralised component was of $-1.0 \mu\text{V}$ ($p < .0001$) in the HiS group and $-.8 \mu\text{V}$ ($p < .0001$) in the LoS group. More interesting, in the case of late N2pc time period (232–272 ms), the N2pc was of $-1.2 \mu\text{V}$ ($p < .0001$) in the HiS group and negligible in LoS

individuals ($-0.3 \mu\text{V}$, $p = \text{ns}$). To isolate the N2pc component from the overlapping bilateral ERP components and directly compare the magnitude of the N2pc between the two groups, contralateral-minus-ipsilateral difference waves were computed as shown in Fig. 3C. N2pc amplitude and peak latency were measured from these waveforms. The magnitude of the overall N2pc was substantially larger in the HiS compared to the LoS group (-1.1 vs. $-0.6 \mu\text{V}$), with a significant main effect of Group with $F_{(1, 30)} = 6.69$, $p < .05$, $\eta^2 = .18$. There was a significant Group $\times$ Time period interaction $F_{(1, 30)} = 6.26$, $p < .05$, $\eta^2 = .17$. Post-hoc pairwise comparisons revealed that in the early-phase N2pc time period (191–231 ms) the magnitude was similar between the HiS and LoS groups (-1.0 vs. $-0.8 \mu\text{V}$, $p = \text{ns}$), however this component was longer lasting for the HiS group as shown by the significant difference in the late N2pc time period (232–272 ms) between the two groups (-1.2 vs. $-0.3 \mu\text{V}$, $p < 0.005$). No other main effects or interactions were significant. Group $\times$ Cue-Target location interaction $F_{(4, 120)} = 0.69$, $p = \text{ns}$, $\eta^2 = .02$. Group $\times$ Cue-Target location $\times$ Time period interaction $F_{(4, 120)} = 1.57$, $p = \text{ns}$, $\eta^2 = .05$. N2pc peak latency ($\pm\text{SE}$) was 237.4 ± 3.8 ms in the HiS group and 227.5 ± 2.8 ms in the LoS group. This difference was significant $t_{(30)} = 2.09$, $p < 0.05$ (2-tailed). Thus, it took slightly longer for HiS individuals to allocate the maximum amount of attention to focus on a salient target object compared with LoS individuals.

3.2.2 Mismatch-triggered negativity component

Grand average ERP waveforms at all ROIs are shown in Fig. 4 whereas ERP waveforms separate for the FCL/R, CP/R and POL/R ROIs are shown in Supplementary Figure S3.

< Figure 4 about here > < Inline Supplementary Figure S3 about here >

Fig. 4A shows separate waveforms for match and mismatch trials. For both HiS and LoS groups, an enhanced negativity can be seen for mismatch trials starting at about 350 ms and lasting up to 550 ms post-stimulus at all ROIs. The time period chosen for analyses is indicated by two grey vertical lines, with the onset latency indicated by the first line.

Across all participants, the mismatch-triggered negativity onset was 344 ms with $t_{(31)} = 2.84$, $p < .01$. For HiS individuals it was 336 ms with $t_{(15)} = 3.05$, $p < .01$ and for LoS individuals it was 373 ms with $t_{(15)} = 3.06$, $p < .01$. The ANOVA conducted to test the difference in mismatch-triggered negativity onset between HiS and LoS individuals revealed a significant Group $\times$ Time point interaction $F_{(1.6, 47.1)} = 3.49$, $p < .05$, $\eta^2 = .10$. Thus, HiS generates detectable neural activity 37 ms earlier, which may indicate a general increase in the amount of attentional resources devoted to perform the S1–S2 match/mismatch discrimination after suppressing the irrelevant distractor input.

The ERP waveform for HiS individuals is more enhanced compared to LoS individuals for mismatch trials than for match trials, and this observation reached statistical significance in the form of an interaction between Group and Trial Type with $F_{(1, 30)} = 6.25$, $p < .05$, $\eta^2 = .17$. The mean amplitude of mismatch-triggered negativity was of $-2.5 \mu V$ ($p < .0001$) in the HiS group and $-1.1 \mu V$ ($p < .01$) in LoS individuals. In order to directly compare the mismatch-triggered negativity between the two groups, mismatch-minus-match trials difference waves were computed as shown in Fig. 5B. The mean amplitude of the component was measured from these waveforms. The magnitude of the mismatch-triggered negativity, was substantially larger in the HiS compared to the LoS group, with a significant main effect of Group with $F_{(1, 30)} = 6.25$, $p < .05$, $\eta^2 = .17$. This result confirms that the mismatch-triggered negativity extended to all ROIs and was significantly larger in the HiS group compared with LoS group, between 344 and 544 ms (-2.5 vs. $-1.1 \mu V$, $p < 0.05$). This

pattern probably reflects an overspread of activation in HiS individuals relative to LoS individuals. No other main effects or interactions were significant. Group $\times$ Cue-Target location interaction $F_{(4, 120)} = 1.00, p = ns, \eta p2 = .00$. Group $\times$ Cue-Target location $\times$ Hemisphere interaction $F_{(4, 120)} = 1.15, p = ns, \eta p2 = .04$. Group $\times$ Cue-Target location $\times$ Sagittal Axis interaction $F_{(8, 240)} = 0.83, p = ns, \eta p2 = .02$. Group $\times$ Cue-Target location $\times$ Sagittal Axis $\times$ Hemisphere interaction $F_{(8, 240)} = 1.40, p = ns, \eta p2 = .04$.

3.3 Correlations between Schizotypy personality traits and ERPs measures

The Pearson's product moment correlations between the sub-scales of O-LIFE questionnaire and electrophysiological measures of attentional processes are reported in Table 2. O-LIFE subscales were positively inter-correlated with each other. These results accord with the reported extensive norms (Mason and Claridge, 2006) but show stronger correlation coefficients, probably because the selected participants were extreme scores.

< Table 2 about here >

Unusual Experiences was found to be significantly negatively related to larger late-phase N2pc amplitude at parieto-occipital ROIs and positively related to larger mismatch-triggered negativity amplitude at all ROIs. A hierarchical multiple regression analysis was conducted to identify the predictors of Schizotypy. Two different models were examined. In the first model the late phase of N2pc explained a significant proportion of variance in *Unusual Experiences* scores, $R^2 = .21, F_{(1, 30)} = 8.11, p < .01$. In the second model, the inclusion of mismatch triggered negativity has significantly increased the predictive capacity of overall *Unusual Experiences* score, R^2 change = .19, $F_{(1, 29)} = 9.44, p < .005$. In the second model the late phase of N2pc amplitude significantly predicted *Unusual Experiences* scores,

$\beta = -4.86$, $t_{(29)} = -3.37$, $p < .005$. The mismatch triggered negativity also significantly predicted *Unusual Experiences* scores, $\beta = 2.09$, $t_{(29)} = 3.07$, $p < .005$. The second model, where both ERP measures that distinguished between HiS and LoS individuals were entered as independent predictor variables, explained in combination a greater proportion of variance in *Unusual Experiences* scores, $R^2 = .41$, $F_{(2, 29)} = 9.92$, $p < .001$.

Cognitive Disorganisation was significantly positively correlated with longer N2pc peak latency at parieto-occipital ROIs. *Impulsive Non-conformity* scores was found to be negatively and significantly correlated with larger late-phase N2pc amplitude at parieto-occipital ROIs, indicating that an average increase in this scale was associated with a decrease of positivity (increase of negativity) in the amplitude of N2pc component. However, there was no significant correlation between the ERP components with negative schizotypy ('*Introverted Anhedonia*'). Overall this pattern of correlations suggests that the schizotypal personality traits are associated with the specific attentional processes assessed with the two ERP components of late phase of N2pc and mismatch triggered negativity (See Table 2). Figure 5 shows the dispersion of the data and the regression slopes of the significant correlations between schizotypal scores, as measured with O-LIFE, and attentional processes, as measured with ERPs.

< Figure 5 about here >

Fisher's z test comparing correlation coefficients between the two independent groups of HiS and LoS individuals revealed a significant groups difference in the correlation coefficients between *Cognitive Disorganisation* and both the early and late phase of N2pc amplitude at parieto-occipital ROIs. In the case of the early phase of N2pc (191-231 ms) HiS individuals showed a positive correlation ($r = .467$) and LoS showed an opposite, negative correlation ($r = -.417$), with $Z_{(30)} = 2.423$, $p < .05$ (two-tailed). A similar pattern of results was

found in the case of the late phase of N2pc (232-272 ms) with HiS individuals showing a positive correlation ($r=.376$) and LoS showed an opposite, negative correlation ($r=-.362$), with $Z_{(30)} = 1.976$, $p < .05$ (two-tailed). This result indicates that, for HiS, an average increase in this sub-scale scores was associated with an increase of positivity (decrease of negativity) in the magnitude of the N2pc. For LoS, an average increase in *cognitive disorganisation* scores was associated with a decrease of positivity (increase of negativity) in the magnitude of N2pc. Figure 6 shows the dispersion of the data and the slopes of linear regression for each group of the significant differences in correlation coefficients between *Cognitive Disorganisation* scores and attentional processes as measured with the N2pc component. No other significant Fisher's z test results were found comparing correlation coefficients between the two groups. See Supplementary Table 1.

< Figure 6 about here > < Inline Supplementary Table S1 about here >

4. Discussion

A broad purpose of the current investigation was to determine which attentional deficits contribute to schizotypal personality traits by individually assessing specific components of attention, defined according to Luck and Gold's (2008) SZ oriented attentional framework. To this end, we used a novel experimental design that combined three paradigms within the context of a single experiment: spatial cueing, visual search and delayed match-to-sample. This experimental procedure was able to provide multiple measures of cognitive processing across two groups of high and low schizotypal participants. Specifically, individuals prone to developing psychosis were facilitated by the task-irrelevant spatial cue while LoS exhibited the more typical pattern of IOR. These behavioural results suggest impairment in rule selection, the selective activation of task-appropriate rules, in HiS individuals. Furthermore, the greater peak latency and amplitude of the late phase of N2pc in the HiS group suggest an

impairment in the implementation of selection. Additionally, the finding of increased magnitude of the perceptually related mismatch-triggered negativity in HiS individuals suggests greater deployment of attentional resources in this group to cope with the demands of the task which requires top-down control to integrate the target's features with representations available in STVM. On the whole, results from the current investigation are consistent with the hypothesis that relative deficits in implementation of selection, mediated by executive control, could lead to an increase of allocated attention to the target's features relevant for the task-set in individuals with schizotypal personality traits.

4.1 Inhibition of return paradigm

Taking into account Luck and Gold's (2008) attentional framework, the IOR paradigm represents a rule-selection task. In our study, the task-irrelevant exogenous spatial cue automatically activates a shift of reflexive attention to its peripheral location. This can be considered a stimulus-driven *exogenous rule* which needs to be inhibited, requiring the involvement of executive control processes to disengage attention from a misleading spatial location and refocus attention at the screen centre. This top-down voluntary process can be considered a task-relevant *endogenous rule*, established by the explicit instruction to constantly fixate centrally and by the uninformative nature of the cue implicitly experienced by participants (i.e. 75% of invalid trials). This idea is supported by a recent study which demonstrated that the visual system systematically tags environmental information during a search in an effort to improve performance in future search events (Lleras et al., 2009). That study found that information leading to search failures (i.e. a shift of attention to a uninformative cue location) is negatively tagged, so as to discourage future deployments of attention towards that information.

In a typical spatial cueing paradigm, the SOA where facilitation gives way to IOR is 293 ms in normal controls and 758 ms in SZ patients, as suggested by meta-analyses of the IOR effect (Mushquash et al., 2012). Here we found that with long SOAs of 700 and 1200 ms LoS individuals showed an IOR effect, HiS individuals showed facilitation (i.e. spatial cueing) rather than the more typical pattern of IOR. Further support of our results in HiS individuals comes from a review of the literature on the orienting of spatial attention in SZ, which suggested that attentional orienting in response to a valid cue might be paradoxically enhanced in SZ patients compared to healthy individuals (Spencer et al., 2011). The current results suggest that HiS individuals experience difficulty in selecting a different rule for the attentional system to follow and might have deficits in input selection tasks when they involve competition between the rules that govern the control of input selection (Luck and Gold, 2008). This hypothesis has been previously supported by a study where SZ patients showed impaired behavioural performance in a variant of the spatial cuing paradigm in which a peripheral cue indicated that the target would appear in the opposite visual field (Maruff et al., 1996).

An important aspect of the present study is that the target was not presented in isolation, as in the majority of spatial cueing paradigms (Larrison et al., 2000), but accompanied by distractor stimuli. In spatial cuing paradigms the effects of cue validity are stronger when accompanied by distractors (Luck et al., 1996). Similarly, the effects of attention at the single neuron level are stronger when a target and a distractor are presented simultaneously with a given neuron's receptive field (Luck et al., 1997a; Moran and Desimone, 1985) and when the target needs to overcome the greater salience of the distractor (Reynolds et al., 1999). Nonetheless, the present spatial cueing abnormalities suggest that HiS individuals, as SZ patients, have impaired voluntary control over attentional processes with a slower disengagement of attention from the task-irrelevant cue (Gouzoulis-Mayfrank

et al., 2006; Gouzoulis-Mayfrank et al., 2004; Kebir et al., 2010; Luck and Gold, 2008; Spencer et al., 2011).

The behavioural results of the two groups in our study differed only in trials in which the target was presented within the same visual field as the cue (above or below). This may be because when the cue and target appeared in opposite visual fields, they were separated by more than 14°, exceeding extrastriate neuron receptive fields (7–10°) (Hopf et al., 2000) and conditioning the level of activation of homologous visual areas of different hemispheres.

4.2 Visual search paradigm

The use of bilateral stimulus arrays containing a lateralised target makes it possible to accurately measure N2pc onset latency, which provides a precise measure of the time of initial shifting of attention towards the task-relevant inputs at which perceptual processing begins to be focused onto the target item in the visual cortex (Luck et al., 1997b; Luck and Hillyard, 1994a; Luck and Hillyard, 1994b; Purcell et al., 2013; Woodman and Luck, 2003). The purpose of using an efficient ‘pop-out’ feature search array of homogeneous distractors (Treisman and Gelade, 1980) in the current study, was to make the control of input selection – referring to the process that guides attention to the location of the task-relevant item – easy. Moreover, since the cue shape (S1) was always the same colour as the target shape (S2), the colour could be stored in STVM, along with the necessary shape information, to set the control of selection parameters for the visual search task (Luck and Gold, 2008). If anything, this would probably serve to make control of input selection easier, ensuring that any abnormalities in the N2pc could not be due to relative deficits in the implementation of selection.

In the current study, we found no difference in N2pc onset latency and early phase N2pc magnitude between groups, suggesting that the early phase of this component, related with the activation of parietal areas to initiate a shift of attention to the location of the task-relevant item (Corbetta et al., 1995; Hopf et al., 2000; Fuggetta et al., 2006), is intact in HiS individuals. These results provide clear evidence that HiS individuals possess the neural circuitry necessary to execute rapid shift of attention towards the salient target location, defined by its colour and shape, as rapidly as LoS individuals.

Furthermore, we observed the late phase of N2pc magnitude to be larger and N2pc peak latency was significantly delayed in HiS individuals than LoS individuals. Our significant late phase N2pc results clash with the interpretation of null results reported by Luck et al. (2006). However, this finding does seem to be hinted at in the N2pc difference waves in figure 4A of Luck et al.'s paper (2006). This result of enhanced and postponed amplitude of late phase N2pc which is implemented by extrastriate areas of the occipital and inferior temporal cortex (Hopf et al. 2000 and Hopf et al. 2006), suggests an impairment in the implementation of selection – referring to the process that enhances the task-relevant features of target and suppresses the irrelevant inputs – in HiS individuals. Thus, the present results in HiS individuals contrast with previous claims that implementation selection is largely intact in SZ patients (Luck et al., 2006; Luck & Gold, 2008).

Nevertheless, it should be remembered that there are some key differences between the current experiment and those discussed by Luck and Gold (2008). In the present investigation, we used a combination of a delayed match-to-sample paradigm, a spatial cueing paradigm and a visual search paradigm. Our task involved a higher-level of attentional control processes as it included an STVM component that may have strained the attentional system to which it is linked. In addition, there was a task-irrelevant spatial cue which altered

the distribution of visual–spatial attention prior to the search array onset in a rule-selection task (i.e. spatial cueing). Thus it is plausible that these factors may have stressed the implementation of selection process more than other tasks, with a consequent greater involvement of neural networks, hence the greater late phase N2pc amplitudes.

Good evidence has been accumulated that the N2pc is modulated by feedback from top-down systems and is sensitive to attentional demand of the search task (Eimer, 1996; Hopf et al., 2002; Luck et al., 1997b; Luck and Hillyard, 1994a; Wykowska & Schubö, 2010; Wykowska & Schubö, 2011). This hypothesis has been directly tested in a series of studies into the neural basis of the N2pc component by simultaneously recording intracranially and extracranially from macaque monkeys (Cohen et al., 2009; Purcell et al., 2013; Woodman et al., 2007a). Results are consistent with the concept that early frontal eye field (FEF) activity modulates later neural activity in posterior visual regions during both inefficient and efficient (i.e. pop-out) searches. It is important to note that the monkey-N2pc depended on prefrontal cortex activity even during an efficient search task requiring minimal feature analyses (Purcell et al., 2013). These results are consistent with a growing body of work demonstrating the sensitivity of N2pc to top-down factors and suggest that FEF is likely a source of this top-down modulation (An et al., 2012; Bichot et al., 2001; Bichot and Schall, 1999; Bichot and Schall, 2002; Ding and Hikosaka, 2006; Eimer and Kiss, 2010; Eimer et al., 2009; Kiss et al., 2009; Pouget et al., 2009; Purcell et al., 2013). For example, trial history, prior knowledge, expectation and experience have a strong influence on pop-out performance in both the human N2pc (An et al., 2012; Eimer and Kiss, 2010; Eimer et al., 2010) and FEF neurons of monkeys trained to perform pop-out visual search tasks during which short-term priming is typically caused by the repetition of stimulus features and target position (Bichot and Schall, 1999; Bichot and Schall, 2002).

4.3 Match-to-sample paradigm

In the match-to-sample task in the current study the singleton was always task-relevant, therefore attention directed towards the target was a combination of both bottom-up target salience and the top-down task set. Taking into account Luck and Gold's (2008) conceptual framework for attention, when the cue shape (S1) appeared, observers stored its identity in STVM. Then executive processes sent control parameters to the input selection system that determined what types of inputs should be selected. These parameters caused attention to be guided to the relevant-features of the to-be detected target shape (S2) (i.e. control of input selection), which in turn caused attention to focus on the target, facilitating processing of the attended target's features such as colour and shape, and inhibiting processing of the unattended distractor inputs (i.e. implementation of input selection) (Chelazzi et al., 1998; Woodman et al., 2007b).

Previous results from our lab (Bennett et al., 2014) with healthy individuals using a very similar delayed match-to-sample task to the current study have shown that the presence of distractors substantially increases error rates, RTs and also the magnitude and duration of the mismatch-triggered negativity in mismatch compared with match trials. It seems that the establishment of a 'target mismatch' response is harder while enhancing the relevant target input (Mazza et al., 2009) or suppressing irrelevant distractors (Luck and Hillyard, 1994a; Luck and Hillyard, 1994b). Under these conditions of multiple sources of perceptual mismatch, participants must exert greater top-down control on input selection processes to guide attention to the task-relevant target (i.e. control of selection), to enhance the target's features and simultaneously to suppress the irrelevant distractors (i.e. implementation of selection).

In the current study, HiS individuals displayed a significantly greater mismatch-triggered negativity magnitude than LoS individuals which was associated with earlier onset latency in the HiS group. One possible hypothesis for the greater mismatch-triggered negativity in healthy individuals with HiS traits as compared with LoS individuals, is that the former experienced increased attentional demands during this task and deployed greater attentional resources with overspread of activation for their relative deficits in executive functions in the attempt to successfully integrate the visual representation of the target with the existing representations of cue shape (S1) available in STVM. This integration process was also particularly difficult for HiS individuals possibly due to the relative deficits in their implementation of selection process occurring at 232–272 ms (late phase N2pc). A similar interpretation of overspread of activation has been put forward in a previous study which found enhanced amplitude of N400 on individuals with high schizotypal traits performing a semantic categorisation task previously used with SZ patients (Prevost et al., 2010). The RT and accuracy data of the current study suggest that HiS individuals performed the task as well as LoS individuals. The lack of correspondence between the behavioural effects and the ERP effects seem to suggest that HiS individuals may adopted a compensatory strategy to effectively perform the task in spite of their attention deficits. However more empirical evidence is needed to demonstrate the presence of such compensatory mechanisms (See Limitations).

4.4 Correlations between Schizotypy personality traits and ERPs measures

A purpose of the current study was to find direct electrophysiological correlates of schizotypal personality traits by examining their relationship with ERP components. The results of correlational analyses in the whole group (merging HiS and LoS participants) suggest that the late phase of N2pc magnitude may be useful in assessing the likelihood of a person exhibiting the positive (*Unusual Experiences*) schizotypy and *Impulsive Non-*

conformity. The magnitude of mismatch-triggered negativity component also showed to be associated with the *Unusual Experiences* sub-scale of O-LIFE questionnaire (Mason and Claridge, 2006; Mason et al., 1995). By performing a multiple hierarchical regression analyses we could establish that both ERP measures of attentional process are strong predictors of positive schizotypy and if used in combination are able to significantly increase their overall predictive capacity in assessing individuals undergoing hallucinatory experiences, unusual perceptual aberrations, and magical thinking.

The N2pc peak latency showed to be related to the disorganised (*Cognitive Disorganisation*) schizotypy in the whole group. The results of comparing correlation coefficients between HiS and LoS individuals suggest that the N2pc magnitude may be a useful direct electrophysiological measure to distinguish individuals from the general population exhibiting extremely low or high '*Cognitive Disorganisation*' scores. In particular, these results indicate that, for HiS, an average increase in *Cognitive Disorganisation* sub-scale was associated with an increase of positivity (i.e. decrease of magnitude) in the N2pc component (See Figure 6). Since the N2pc represents an electrophysiological correlate of the focusing covert attention on a peripheral target location (Eimer, 1996; Kiss et al., 2008; Luck and Hillyard, 1994a; Luck and Hillyard, 1994b; Mazza et al., 2009; Woodman and Luck, 1999; Woodman and Luck, 2003), these results suggest that HiS individuals scoring higher in the disorganised trait of schizotypy are showing a progressive degree of deficits in focusing of attention to perform an in-depth analysis of the target's features for further processing (i.e. relative deficit in input selection processes). The opposite pattern holds for LoS, indicating that an average increase in this scale was associated with a decrease of positivity (i.e. increase of magnitude) in the amplitude of N2pc component (See Figure 6). Overall these results suggest that the opposite association in LoS compared to HiS, between their correlations between cognitive disorganization scores and

ERPs measures in the N2pc time window are showing that the most efficient attentional mechanisms represented by the more typical magnitude of N2pc component belongs to those individuals of both groups who lie towards the mid-range of cognitive disorganisation sub-scale scores which are closer to those reported in the extensive norms (Mason and Claridge, 2006).

On the whole, the correlation results suggest that if the N2pc reflects the process of implementation of attention by extrastriate areas of the occipital and inferior temporal cortex (Hopf et al. 2000 and Hopf et al. 2006), then the relationship between individuals undergoing *Unusual Experiences/Cognitive Disorganisation* and amplitude of N2pc could be an indication of a putative link between the positive/disorganised aspects of schizotypy and impairment of occipital and inferior temporal cortex function. Healthy participants scoring highly on each of the two sub-scales *Unusual Experiences* and *Cognitive Disorganisation* typically demonstrate the same pattern of neuro-cognitive deficits as the SZ patients, with pronounced positive or disorganized symptomatology (Rawlings and Goldberg, 2001; Goodarzi et al, 2000). The correlation results on the amplitude of mismatch-triggered negativity also suggest that if this component evoked by stimuli' perceptual mismatch does reflect a frontal lobe function (Folstein and Van Petten, 2008; Zhang et al., 2008), and positive traits in schizotypy are related to a frontal lobe hypo-function, then the relationship between positive schizotypy and amplitude on mismatch-triggered negativity could be an indication of a link between positive schizotypy and impairment of frontal lobe function. Overall, this pattern of correlations suggests that the specific deficits of implementation of attention and integration processes as assessed with two ERP components of N2pc and mismatch-triggered negativity were primarily associated with the positive and disorganised dimensions of schizotypy as assessed with the O-LIFE questionnaire (Mason and Claridge, 2006; Mason et al., 1995). Previous research has also suggested that that ERPs may be used

to study neurocognitive processes and distinguish individuals with high and low schizotypal traits in healthy populations (Debruille et al., 2013; Gassab et al., 2006; Kiang and Kutas, 2005; Prevost et al., 2010; Wan et al., 2006).

4.5 Limitations

A limitation of the current study is that we could not exclude the possibility that any effect occurring at the mismatch-triggered negativity could have been primarily determined by a deficit in initial allocation of attention to the target occurring over the N2pc. Further work (e.g. using a central target) will be able to disentangle a direct deficit of the mismatch-triggered negativity from an indirect “knock-on” effect from a deficit in the cognitive processes represented by the preceding N2pc.

Another limitation of this study is represented by the absence of a significant behavioural difference between the two groups despite significant differences in both late phase of N2pc and mismatch-triggered negativity components. We discussed that HiS individuals may adopted a compensatory strategy to effectively perform the task in spite of their relative deficits. In order to demonstrate the presence of such compensatory mechanisms, further work is needed. It would be necessary to design an input selection task which involves a stronger competition between the rules that govern the control of selection and provides a greater challenge to the selection process (e.g. using an additional task combined with the paradigm used in this study). This paradigm, which requires greater involvement of top-down control processes, could lead to behavioural effects with worse performance for HiS as compared to LoS participants for the failure of compensatory mechanisms to override their relative deficits of both control and implementation of selection.

4.6 Conclusions

In the current study, we adopted Luck and Gold's (2008) framework to assess the specific deficits in attention processes that characterise individuals with schizotypal personality traits. To this end we combined a spatial cueing paradigm, a memory-guided efficient visual search paradigm and a delayed match-to-sample paradigm in a single experimental procedure.

Overall, the results of increased amplitude in ERP components in the current study suggest an “overspread of activation” in HiS individuals during the execution of a quite demanding attention task. It seems that relative deficits in their top-down control processes lead to deficits in both rule selection and input selection processes — requiring precise focusing of attention to perform an in-depth analysis of the target's features for further processing. The mismatch-triggered negativity ERP component, which was increased in HiS individuals, suggests greater deployment of attentional resources in order to compensate for the demanding task which requires top-down control of input selection to integrate the target's features with representations available in visual working memory. To conclude, the results of this electrophysiological study suggest that the ERP measures of late phase of N2pc and mismatch-triggered negativity could serve as potential markers of individuals among the general population with a high-risk of developing psychosis. These findings support the fully dimensional model, which posits that varying levels of schizotypal personality traits throughout the general population lie on a continuum of SZ spectrum disorders (Nelson et al., 2013). The implications of the results for putative attention deficits underlying schizotypy can serve to motivate further research on more specific cognitive and perceptual mechanisms that are impaired in, and might be responsible for, the positive and disorganised symptomatology in SZ.

Contributors

G. Fuggetta was responsible for all aspects of study design, data collection, experimental methods, signal analyses, statistical analysis, data interpretation, and manuscript preparation. M. Bennett participated directly in data collection, data interpretation and manuscript preparation. P. Duke was responsible of programming the task, experimental methods, data interpretation and manuscript preparation. All authors contributed to and approved the final manuscript.

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Table and Figure captions

Fig. 1. Example of a sequence of events of one trial of the experiment. Subjects' task was to indicate whether the first shape (S1) matched or mismatched the target shape (S2). This trial is an example of mismatch condition because the first shape (S1) (green diamond) is different from the target shape (S2) (green hexagon). Moreover this trial is an example of uncued condition where the position cue (white star) appears in an adjacent quadrant below the upcoming target shape.

Fig. 2. (A–B–C–D) Mean of RT ($\pm$ SEM) difference values to examine the attentional effects of the task-irrelevant and uninformative cues for both groups of participants. (A) HiS individuals displayed a spatial cueing effect, whilst LoS individuals showed the more typical IOR effect. These significant effects were revealed by subtracting RT values of trials where cues appeared in an adjacent quadrant above/below the target (invalid trials with vertical deviation) from those obtained when the cue appeared in the same locations of the incoming target (valid trials) * $p < .05$.

Fig. 3. (A–B) Grand average ERP lateralised waveforms from experiment at parieto-occipital sites. Negative is plotted upward. Contralateral waveforms were computed by averaging left-target waveforms at right-hemisphere electrode sites with right-target waveforms at left-hemisphere electrode sites. Ipsilateral waveforms were computed by averaging left-target waveforms at left-hemisphere electrode sites with right-target waveforms at right-hemisphere electrode sites. (C) Grand average contralateral-minus-ipsilateral difference waveforms, averaged across the left and right parieto-occipital ROIs.

Late phase of N2pc, had a greater peak latency and amplitude in the HiS group as compared to LoS group. Vertical lines in all plots indicate time periods chosen for analyses. ** $p < .01$.

Fig. 4. (A) Grand average ERP bilateral waveforms separated by match and mismatch trials, averaged across fronto-central, centro-parietal and parieto-occipital ROIs. Negative is plotted upward. (B) Grand average mismatch-minus-match difference waveforms. HiS individuals exhibited earlier onset and greater and sustained amplitude of the mismatch-triggered negativity component as compared to LoS individuals. Vertical lines in all plots indicate the time period chosen for analyses. * $p < .05$.

Fig. 5. Scatterplots with line of best fit for the entire group relating ERP measures which differentiated LoS from HiS individuals and the dimensions of O-LIFE questionnaire.

Fig. 6. Scatterplots with line of best fit separate for HiS and LoS groups relating early and late phases of N2pc ERP component and the Cognitive Disorganisation sub-scale of O-LIFE questionnaire.

Table 1. Demographic information of subjects with varying levels of schizotypy personality traits.

Table 2. Correlation analysis of the relationship between O-LIFE and ERP measures (N=32)

Supplementary Table 1. Fisher's z test results comparing correlation coefficients between two independent groups.

Fig. S1. (A) Mean ($\pm$ SEM) RTs and (B) mean ($\pm$ SEM) error rates for both groups of participants. The figure shows that both groups of participants have very similar behavioural performances with significant greater performance in matching compared to mismatching trials. *** $p < .001$; ** $p < .01$; * $p < .05$.

Fig. S2. (A–B) Grand average ERP lateralised waveforms from experiment at PO7/8 electrodes. Negative is plotted upward. (C) Grand average contralateral-minus-ipsilateral difference waveforms, averaged across PO7/8 electrodes. Late phase of N2pc, had a greater peak latency and amplitude in the HiS group as compared to LoS group. Vertical lines in all plots indicate time periods chosen for analyses. ** $p < .01$.

Fig. S3. (A1– B1–C1) Grand average ERP bilateral waveforms separated by match and mismatch trials. Negative is plotted upward (A2– B2–C2). Grand average mismatch-minus-match difference waveforms: fronto-central sites (A2); centro-parietal sites (B2); and parieto-occipital sites (C2). HiS individuals exhibited earlier onset and greater and sustained amplitude of the mismatch-triggered negativity component as compared to LoS individuals. Vertical lines in all plots indicate the time period chosen for analyses. * $p < .05$.

Shape Cue: 500 ms

Fixation: 450 or 550 ms

Position Cue: 100 ms

Delay: 600 or 1100 ms

Target Array: 150 ms

Response: ∞ ms

Fig 1

A

B

C

D

Fig 2

Fig 3

Fig 4

Fig 5

Fig 6

Sup Fig 3

Table 1. Demographic information of subjects with varying levels of schizotypy personality traits.

	High Schizotypy (<i>N</i> =16)	Low Schizotypy (<i>N</i> =16)	Statistics
Age (years)	19.80 (1.19), 19.71 (18.25-22.17)	20.46 (1.93), 20.13 (18.33-25.50)	<i>t</i> (30) = -1.16, <i>p</i> = ns ^a
Gender (Male, Female)	3, 13	2, 14	χ^2 (1) = 0.24, <i>p</i> = ns ^a
Handedness (Left, Right)	1, 15	1, 15	χ^2 (1) = 0.00, <i>p</i> = ns ^a
Unusual Experiences score	15.31 (6.28), 16.00 (2-23)	3.25 (3.64), 1.50 (0-12)	<i>U</i> (30) = 14.5, <i>p</i> < .001 ^a
Cognitive Disorganisation score	17.69 (6.49), 19.50 (2-24)	6.88 (4.81), 6.50 (0-16)	<i>U</i> (30) = 25.5, <i>p</i> < .001 ^a
Introvertive Anhedonia score	10.56 (6.54), 8.50 (1-20)	4.88 (5.02), 3.00 (0-15)	<i>U</i> (30) = 56.5, <i>p</i> < .01 ^a
Impulsive Nonconformity score	11.00 (3.71), 11.00 (2-16)	5.44 (3.76), 6.00 (0-13)	<i>U</i> (30) = 40.0, <i>p</i> < .001 ^a

Values are mean (SD), median (minimum-maximum), unless otherwise indicated.

ns non-significant; ^a T-test, Chi-square test, Mann-Whitney *U* test, and ANOVA *F* test, accepted at the .05 level of significance (2-tailed).

Table 2. Correlation analysis of the relationship between O-LIFE and ERP measures (N=32)

	2. Cognitive Disorganisation	3. Introverted Anhedonia	4. Impulsive Nonconformity	5. N2pc peak latency L/R parieto-occipital ROIs	6. N2pc mean amp. 191-231 ms parieto-occipital ROIs	7. N2pc mean amp. 232-272 ms parieto-occipital ROIs	8. Mismatch-triggered-negativity mean amp. 344-544 ms all ROIs
1. Unusual Experiences	.702**	.297 ns	.637**	.310 ns	-.116 ns	-.461**	.417*
2. Cognitive Disorganisation	—	.451**	.641**	.360*	-.088 ns	-.348 ns	.209 ns
3. Introverted Anhedonia		—	.450**	.029 ns	.112 ns	-.082 ns	.199 ns
4. Impulsive Nonconformity			—	.293 ns	-.074 ns	-.366*	.287 ns
5. N2pc peak latency L/R parieto-occipital ROIs				—	.194 ns	-.447*	-.179 ns
6. N2pc mean amp. 191-231 ms parieto-occipital ROIs					—	.464**	-.176 ns
7. N2pc mean amp. 232-272 ms parieto-occipital ROIs						—	.048 ns
8. Mismatch-triggered-negativity mean amp. 344-544 ms all ROIs							—

Region of Interest (ROI); ns non-significant; * $p < .05$; ** $p < .01$ (2-tailed).