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Face repetition detection and social interest: An ERP study in adults with and without Williams syndrome

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Abstract

The present study examined possible neural mechanisms underlying increased social interest in persons with Williams syndrome (WS). Visual event-related potentials (ERPs) during passive viewing were used to compare incidental memory traces for repeated vs. single presentations of previously unfamiliar social (faces) and nonsocial (houses) images in 26 adults with WS and 26 typical adults. Results indicated that participants with WS developed familiarity with the repeated faces and houses (frontal N400 response), but only typical adults evidenced the parietal old/new effect (previously associated with stimulus recollection) for the repeated faces. There was also no evidence of exceptional salience of social information in WS, as ERP markers of memory for repeated faces vs. houses were not significantly different. Thus, while persons with WS exhibit behavioral evidence of increased social interest, their processing of social information in the absence of specific instructions may be relatively superficial. The ERP evidence of face repetition detection in WS was independent of IQ and the earlier perceptual differentiation of social vs. nonsocial stimuli. Large individual differences in ERPs of participants with WS may provide valuable information for understanding the WS phenotype and have relevance for educational and treatment purposes.

Keywords

ERP; face; familiarity; memory; Williams syndrome

Williams syndrome (WS) is a genetic disorder caused by a deletion of at least 24 genes on chromosome 7 (Hillier et al. 2003). It occurs in ~1 in 7,500 live births (Strømme et al., 2002) and results in mild to moderate intellectual disabilities (see Martens et al. 2008 for a review) with deficits in visuo-spatial processing and construction abilities and relative strengths in the verbal domain (e.g., Wang & Bellugi, 1994; Jarrold et al., 2001; Mervis et al. 2000; Karmiloff-Smith et al., 2003).

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One prominent feature of the WS behavioral phenotype is hypersociability (Bellugi et al., 2007; Fishman et al., 2011; Mervis & Klein-Tasman, 2000), which manifests as indiscriminate friendliness (see Jarvinen et al., 2013 for review). Similar to typical peers, persons with WS rate familiar faces as more approachable than unfamiliar ones (Jarvinen-Pasley et al., 2010). However, they also often view strangers as more approachable (Doyle et al., 2004; Jones et al., 2000; Martens et al., 2009; Fishman et al., 2011), although such exaggerated approachability could be limited to strangers with happy facial expressions (Frigerio et al., 2006).

The exact reasons for the increased social approach behavior exhibited by many persons with WS are not yet fully understood. Suggested explanations to date include difficulties inhibiting responses to social information (Porter et al., 2007), atypical perceptual processing of faces (Jarvinen-Pasley et al., 2010), or atypically increased salience of social stimuli (Frigerio et al., 2006). Considerable previous research in WS has documented enhanced attention to faces (Riby et al., 2011; Plesa-Skwerer et al., 2009, 2011; Doherty-Sneddon et al., 2009), especially the eyes (Jones et al., 2000; Mervis, 2003; Riby & Hancock, 2008), atypically long fixations on faces and difficulty disengaging from human faces (Riby & Hancock, 2009; Riby et al., 2011). Face perception in WS appears relatively intact when assessed with unique tasks (Tager-Flusberg et al., 2003) or standardized measures of face processing (e.g., Benton Test of Face Recognition - Bellugi et al., 1994, Wang et al., 1995; Rivermead Behavioral Memory Test – Udwin & Yule, 1991; Mooney Face Test – Bellugi et al., 1988). However, developmental delays and/or atypical perceptual processing strategies have also been reported, including increased focus on face parts, deficits in configural processing (Deruelle et al., 1999; Karmiloff-Smith et al., 1997, 2004), and difficulties with identifying complex emotional expressions (Jarvinen-Pasley et al., 2010).

Despite this body of work, it remains challenging to evaluate the extent of social interest in persons with WS. Grelotti et al. (2002) proposed that “social interest ... underlies or accompanies all processes that deal with the face. ... without this natural influence there is little to prime us to look at faces with any more frequency than other objects” (p.219). However, most studies to date have actively directed participants’ attention to faces for the purpose of identifying emotions, evaluating approachability, or memorizing for subsequent recognition. An alternative approach involves examining responses to faces when individuals are not explicitly instructed to attend to them. For example, Plesa-Skwerer et al. (2011) utilized self-selected viewing time as an indirect measure of interest in complex social and nonsocial images. They observed that participants with WS spent more time looking at social than nonsocial images, while typical controls did not differ in the viewing time for the two stimulus categories. However, Riby et al. (2011) found no group differences in the distracting effect of faces when participants with and without WS engaged in visual search for a non-face target.

Behavioral and neuroimaging studies have repeatedly demonstrated that motivational salience affects multiple stages of stimulus processing, such as orienting, attention, and memory (for reviews see Bromberg-Martin et al., 2010; Gabrieli, 1998; Corbetta & Shulman, 2002). Thus, a more salient stimulus would undergo more extensive cognitive

processing than a less personally relevant stimulus. Measures of brain activity such as event-related potentials (ERP) offer sufficient temporal resolution to examine all stages of stimulus processing, from early sensory responses to later cognitive evaluation, and provide interpretable data even without overt responses by the participant. Recently, we developed a passive repetition-based incidental memory ERP paradigm to examine information processing and stimulus salience in individuals with developmental disabilities (Key & Dykens, 2014; Key & Corbett, 2014). Typically, repeated presentations of identical images in a stream of continuously varying items result in increased familiarity (Jessen et al., 2002), which is a basic form of learning and memory (Yonelinas, 2002). We demonstrated that repetition of a socially salient stimulus (face) among unfamiliar images is reflected in the brain responses even in the absence of specific instructions directing attention to the stimuli (Key & Corbett, 2014). Repeated faces elicited increased parietal positivity within 300–500 ms in typical children, but not in children with autism spectrum disorders (ASD), consistent with the interpretation of low social interest in ASD. Importantly, ERP evidence of repetition detection was independent of participants' IQ.

Our incidental memory paradigm capitalizes on prior ERP studies in typical populations examining stimulus repetition in the context of active memorization. Repeated (“old”) stimuli are known to elicit more positive ERP amplitudes than single (“new”) items, as reflected by smaller (less negative) frontal N400 and larger parietal P600 responses, collectively known as the “old/new effect” (Curran & Cleary, 2003; Duarte et al., 2004). The frontal N400 response is observed in the 300–500 ms range and interpreted to reflect general stimulus familiarity (Curran, 2004; Friedman & Johnson, 2000). The parietal P600 response is associated with recall of information (Nessler et al., 2001; Wilding, 2000) and depth of cognitive processing (Rugg et al., 2000). In studies utilizing face stimuli, the parietal old/new response is present within 300–500ms (MacKenzie & Donaldson, 2007; Nessler et al., 2005), earlier than the typical range of 400–900ms observed for non-face stimuli.

Behavioral and ERP studies of memory for faces in WS are relatively few and suggest that immediate face recognition, such as detection among distracters of faces seen just seconds before or same-different judgment of sequentially presented faces, may be comparable to that of typical controls (Tager-Flusberg et al. 2003; Karmiloff-Smith et al., 2004) but carried out by atypical neural processes associated with face perception (Mills et al., 2000, 2013; Grice et al., 2001). Furthermore, even brief delays (e.g., 2–5 sec) between the study and test periods result in reduced face memory performance for individuals with WS compared to mental age-matched controls (O’Hearn et al., 2009). However, to date no study in persons with WS examined neural processes associated with face memory in the absence of explicit instructions or using passive familiarization protocols.

The purpose of the present study was to examine ERP evidence of incidental memory for repeated faces as a marker of social interest in persons with WS compared to typically developing peers. We hypothesized that even without specific instructions, faces would attract attention and therefore be processed to a greater extent than houses due to their high salience as a social stimulus. Consequently, in all participants, repeated faces would form a stronger memory trace compared to the houses, as reflected by a greater old/new ERP effect within 300–500ms after stimulus onset (smaller frontal N400 and larger parietal positivity).

If persons with WS experience greater than typical social stimulus attraction (e.g., Frigerio et al., 2006), then they would generate a larger old/new effect for repeated faces compared to typical peers. Additionally, as an exploratory aim, we examined the relationship between the old/new ERP responses to faces and the early perceptual responses to social vs. nonsocial stimuli (occipito-temporal N170). The latter set of analyses had relevance for the study of WS in general, as information about brain processing of faces vs. objects in this group remains limited.

Method

Participants

Twenty-six individuals with WS (11 females; M age = 26.00, SD = 8.29 years, range 16–49 years) and 26 typical peers (12 females; M age = 26.93, SD = 8.82 years, range 16–47 years) participated in the study. No participants were excluded due to insufficient ERP data quality. Four participants with WS and six typical peers were left-handed, the rest were right-handed (total M = .47, SD = .71; WS M = .62, SD = .75; TD M = .36, SD = .71) as determined by Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal or corrected-to-normal vision. For participants with WS, the mean total IQ was 69.77 (SD =14.56) with better verbal than nonverbal performance (M verbal = 77.69, SD =12.29; M nonverbal = 68.50, SD =17.36, $t(25)$ =3.307, p =.003, d =.649), assessed using Kaufman Brief Intelligence Test-2 (K-BIT-2; Kaufman and Kaufman 2004). Participants in the typical group were students or college graduates employed in the community, with presumed adequate cognitive and adaptive skills.

All participants (and their parents/guardians when needed) provided written informed consent. The study was conducted with approval from the Institutional Review Board of Vanderbilt University.

Stimuli

Stimuli included 51 color photographs of unfamiliar young adults displaying positive facial affect obtained from a standardized Radboud Faces Database set (Langner et al., 2010), 51 color photographs of unfamiliar houses (façade view, obtained from realtor websites), and a drawing of a yellow smiley face. The on-screen size of the stimuli was 30 cm high and 25 cm wide. From the viewing distance of 90 cm, the stimuli subtended visual angles of 19° (h) × 16°(w). The yellow smiley face was 14.5 cm (9.21°) in diameter.

Electrodes

A high-density array of 128 Ag/AgCl electrodes embedded in soft sponges (Geodesic Sensor Net, EGI, Inc., Eugene, OR) was used to record the ERPs. Electrode impedance levels were at or below 40 kOhm as checked before and after testing. During testing, data were sampled at 250Hz with the filters set to 0.1–100 Hz. All electrodes were referred to vertex and then re-referenced offline during data analysis to an average reference, the recommended reference for high-density arrays (Picton et al., 2000) that has also been used successfully in prior ERP studies of memory (e.g., Curran & Cleary, 2003).

ERP Procedure

All stimuli were presented in random order for 1500 ms with a varied inter-stimulus interval of 1300–1600 ms to prevent habituation and development of trial onset expectations. For each participant, one of the unfamiliar faces and one of the houses were randomly selected and repeated 50 times throughout the experiment, yielding a unique set of repeated images for each participant. The remaining stimuli were presented once. To encourage attention to the stimulus sequence, participants were asked to press a response button when they saw the yellow smiley face (10 trials, brain responses to this stimulus were not included in the analysis). Stimulus presentation was controlled by E-prime (v. 2.0, PST, Inc., Pittsburgh, PA). The entire task included 210 trials and lasted approximately 12 minutes. A researcher was present in the room to monitor participants' behavior. If participants became inattentive or restless, stimulus presentation was suspended until the participant was ready to continue with the task.

Data Analysis

Behavioral Data: To support behavioral observations of participants' attention to the stimulus sequence, number and reaction time of the responses to the smiley face probes were submitted to a one-way ANOVA with the diagnostic group as the between-subject factor.

ERP Data: Collected EEGs were filtered using a 30Hz low-pass filter, segmented on stimulus onset to include a 100-ms prestimulus baseline and a 800 ms post-stimulus interval, and screened for ocular and movement artifacts using an automated algorithm in NetStation followed by a manual review. Data for electrodes with poor signal quality within a trial were reconstructed using spherical spline interpolation procedures. If more than 20% of the electrodes within a trial were deemed bad, the entire trial was discarded. The trial retention rates were comparable across groups and conditions (WS: single face=31.00+/-9.32; repeated face=26.00+/-9.32; single houses=25.77+/-8.67; repeated house=25.77+/-7.58; TD: single face=29.54+/-10.00; repeated face=29.62+/-10.39; single houses=31.00+/-9.66; repeated house=30.62+/-9.91; p 's >.05).

Following artifact screening, individual ERPs for repeated and single presentations of faces and houses were averaged, re-referenced to an average reference, and baseline-corrected. To reduce the number of electrodes in the analysis, only data for the electrode clusters identified as optimal for the frontal N400 and parietal P600 old/new effects, as well as bilateral occipito-temporal N170 face response (see Figure 1) were used in the remaining statistical analyses. These four clusters were selected a priori based on previously published ERP studies of face familiarity (Curran & Hancock, 2007) and our prior work on incidental repetition detection (Key & Dykens, 2014; Key & Corbett, 2014).

Next, to reduce the number of time samples in the analysis, data from clustered electrodes were submitted to a temporal principal components analysis (tPCA) with Varimax rotation (Spencer et al., 1999). The use of the data-driven objective tPCA approach reduced the risk of experimenter bias influencing the identification of individual peaks, which is arguably present when visual peak selection approach is used. The tPCAs reduced 800 ms (200 time samples) of data to a small set of non-correlated components (temporal intervals) accounting

for the maximum variance in the average ERP. The number of factors retained for analyses was chosen using the Scree Test (Cattell, 1966). Boundaries of individual temporal windows were identified using the criterion of factor loadings of $|\geq .6|$ or greater. The identified time intervals were consistent with temporal windows utilized in previously published ERP studies of recognition and recall in visual paradigms (e.g., Curran & Hancock, 2007) and prior ERP studies of face perception in (e.g., Grice et al., 2001).

The resulting factor scores were entered into repeated-measures ANOVAs with Group as the between-subject factor and Stimulus (2: faces, houses) $\times$ Memory condition (2: single, repeated) $\times$ Electrode (4: frontal, parietal, left and right occipito-temporal) within-subject factors with Huynh-Feldt correction. Significant interactions were further explored using planned comparisons (testing differences in response to repeated vs. single presentations of faces within each group) as well as post-hoc one-way ANOVAs and pair-wise t-tests. To address the problem of multiple significance tests, false discovery rate (FDR; Benjamini & Hochberg, 1995) approach was used, and only those follow-up tests that remained significant based on the FDR criteria are reported. Unlike the Bonferroni correction that adjusts alpha levels based on the total number of tests conducted, the FDR method controls for the proportion of incorrect rejections of the null hypothesis among the tests for which the null hypothesis was rejected (i.e., tests with p-values less than .05) and has been used successfully in ERP analyses (Crowley et al., 2012; Key & Corbett, 2014).

Results

Behavioral data

Responses to attention probes (smiley face) revealed that all participants maintained attention to the stimuli during the test session. Although the group difference in the number of responses to the attention probe was significant, $F(1,50)=13.940$, $p<.001$, the practical significance of this difference is small: participants with WS responded to 95.8% of the attention probes, while the typical group had 100% accuracy. There were no group differences in the reaction time (WS: $M=588.83$ ms, $SD=109.05$; TD: $M=571.58$ ms, $SD=115.57$, $p=.286$). Within the WS group, greater accuracy was associated with higher composite IQ, $r=.516$, $p=.007$.

ERP data

The tPCA approach identified five temporal windows accounting for 84.83% of the total variance. Stimulus- and/or condition-related effects were observed for four of the five temporal intervals and are reported below. ERP plots for occipito-temporal, frontal, and parietal locations are presented in Figures 2–4.

108–156 ms (Factor 4, 5.62%)—There was a main effect of Stimulus, $F(1,50)=5.820$, $p=.020$, partial $\eta^2=.104$, and a Stimulus $\times$ Electrode $\times$ Group interaction, $F(3,150)=3.489$, $p=.025$, partial $\eta^2=.065$. Follow-up analyses did not identify any significant group differences in response to any particular stimulus type. Within-group pair-wise comparisons indicated that only typical participants elicited more negative responses to

faces than houses at the right occipito-temporal scalp locations, $t(25)=4.193$, $p<.001$, $d=.822$. This difference did not reach significance in persons with WS.

156–236 ms (Factor 3, 10.20%)—This interval was categorized by the main effect of Memory, $F(1,50)=5.629$, $p=.022$, partial $\eta^2=.101$, as well as by interactions of Memory $\times$ Electrode, $F(3,150)=9.789$, $p<.001$, partial $\eta^2=.164$, and Stimulus $\times$ Electrode $\times$ Group, $F(3,150)=5.425$, $p=.003$, partial $\eta^2=.098$. Memory-related differences were present in the form of more positive P2 amplitudes for repeated vs. single presentations at left and right occipito-temporal locations, $t(51)=2.483$, $p=.016$, $d=.344$ and $t(51)=3.895$, $p<.001$, $d=.540$, respectively. At frontal locations, the direction of differences was reversed, with more negative amplitudes for repeated vs. single items, $t(51)=3.758$, $p<.001$, $d=.521$.

Between-group differences were present for faces at right temporal regions, $F(1,50)=12.500$, $p<.001$ and for houses at frontal, $F(1,50)=13.989$, $p<.001$, as well as left and right occipito-temporal locations, $F(1,50)=7.685$, $p=.008$ and $F(1,50)=29.504$, $p<.001$, respectively. In all cases, persons with WS elicited larger responses compared to typical peers.

Within-group analyses revealed stimulus type differentiation only in participants with WS, for whom larger parietal response were observed for houses than faces, $t(25)=4.926$, $p<.001$, $d=.966$. In typical peers, no stimulus-related differences in ERPs remained significant after the FDR correction.

220–520 ms (Factor 2, 29.252%)—There was the main effect of Stimulus, $F(1,50)=15.291$, $p<.001$, partial $\eta^2=.234$, and a Stimulus $\times$ Memory $\times$ Electrode $\times$ Group interaction, $F(3,150)=3.345$, $p=.036$, partial $\eta^2=.063$. This interval overlaps temporal regions corresponding to frontal and parietal old/new responses. The follow-up analyses are described separately for these two ERP components. The examination of waveform morphology suggested that the parietal response might have been more similar to the P3 component given its maximum prior to 500 ms. Therefore, we will use the P3/600 label for the parietal old/new response.

Frontal N400 (FN400)—In typical participants, detection of repeated compared to single houses was evidenced in less negative FN400 responses, $t(25)=2.973$, $p=.006$, $d=.583$. No FN400 effects for faces reached significance. Participants with WS showed evidence of familiarity with both repeated faces and houses as more negative frontal responses were elicited by single vs. repeated presentations of both stimulus types (faces: $t(25)=3.231$, $p=.003$, $d=.634$; houses: $t(25)=4.381$, $p<.001$, $d=.859$). There were no significant differences in the magnitude of the memory trace (computed as a difference score for repeated-single presentations) for faces vs. houses, $t(25)=-.049$, $p=.961$.

Parietal P3/600—Typical participants evidenced enhanced positive parietal P3/P600 responses only for repeated compared to single presentations of faces, $t(25)=3.465$, $p=.002$, $d=.680$. In persons with WS, parietal effects were observed for repeated houses but in the opposite direction: smaller parietal amplitudes were observed for repeated compared to single presentations, $t(25)=4.552$, $p<.001$, $d=.893$.

Occipito-temporal effects—In addition to the hypothesized frontal and parietal effects, memory-related ERP differences were also observed within 220–520 ms at occipito-temporal locations. In typical participants, more negative right occipito-temporal amplitudes were present for repeated vs. single houses, $t(25)=4.510$, $p<.001$, $d=.885$. Participants with WS evidenced similar discrimination effects bilaterally for repeated vs. single faces and houses (left: faces: $t(25)=2.132$, $p=.043$, $d=.418$; houses: $t(25)=3.304$, $p=.003$, $d=.648$; right: faces: $t(25)=2.454$, $p=.021$, $d=.481$; houses: $t(25)=2.415$, $p=.023$, $d=.474$).

Group differences in memory traces—To better address the research question of possible group differences in memory traces for repeated social and nonsocial information, and also to reduce the number of significance tests, memory for repeated vs. single presentations of faces and houses was quantified as a difference score (repeated – single) at each electrode cluster. Between-group differences were then tested using one-way ANOVAs, which identified greater parietal memory response for faces in typical participants compared to persons with WS, $F(1,50)=5.285$, $p=.026$, while persons with WS evidenced greater than typical differences at frontal regions, $F(1,50)=4.879$, $p=.032$. There were no group differences for houses at any of the four electrode clusters (p 's=.106–.793).

484–800 ms (Factor 1, 34.203%)—Although this interval overlaps the possible window for the parietal old/new response, it did not include a clearly defined positive deflection. There was a main effects of Stimulus, $F(1,50)=4.367$, $p=.042$, partial eta sq=.080, as well as Stimulus $\times$ Memory $\times$ Electrode, $F(3,150)=5.802$, $p=.002$, partial eta sq=.104, and Memory $\times$ Electrode $\times$ Group, $F(3,150)=3.244$, $p=.029$, partial eta sq=.061, interactions. Repeated faces and houses were associated with smaller parietal responses compared to single stimuli, $t(51)=2.324$, $p=.024$, $d=.322$ and $t(51)=3.035$, $p=.004$, $d=.421$. More positive responses for repeated vs. single houses were observed at frontal locations, $t(51)=3.546$, $p=.001$, $d=.492$. There were no significant group differences in response to repeated or single stimuli at any of the electrode locations. Within-group analyses noted that only typical participants elicited more positive amplitudes in response to repeated vs. single stimuli at frontal locations, $t(25)=2.694$, $p=.012$, $d=.528$, while the direction of differences was reversed at parietal, $t(25)=4.338$, $p<.001$, $d=.851$, and right occipito-temporal locations, $t(25)=2.570$, $p=.017$, $d=.504$. No memory-related differences reached significance for participants with WS.

Brain-Behavior and Brain-Brain connections

Correlational analyses examined the associations between the brain indices of stimulus repetition detection (frontal and parietal old/new effects for faces and houses), perceptual processes (occipito-temporal N170 difference for faces vs. houses), age, accuracy and RT for the attention probe. No significant correlations were observed for the combined sample or within each group. For participants with WS, these ERP responses also did not correlated with IQ.

Discussion

This study examined frontal and parietal ERP old/new responses to incidental repetitions of faces and houses as an index of social interest in persons with WS and typical peers during

passive viewing of novel stimuli. Based on the ideas that social interest underlies all face-related processes (Grelotti et al., 2002) and that motivational salience increases the extent of stimulus processing (Bromberg-Martin et al., 2010), we hypothesized that even without explicit memorization instructions, repeated faces should be associated with a stronger memory trace than repeated houses. Furthermore, this response should be greater in participants with WS if they experience increased social interest compared to their typical peers.

In participants with WS, both repeated faces and houses elicited the frontal old/new effect (FN400), but there were no significant differences in the magnitude of that response between the two stimulus types. Conversely, in typical adults, the frontal response was evident for the repeated houses, while the parietal old/new effect was observed for the repeated faces. For all participants, ERP indices of memory for the repeated face were independent of the earlier perceptual responses differentiating social from nonsocial stimuli. Additionally, within the WS group, ERP responses indexing memory and perceptual processes were not correlated with age or IQ.

Stimulus-specific memory differences in ERPs were observed in the 220–520 ms period, consistent with prior studies involving active memorization (MacKenzie & Donaldson, 2007; Nessler et al., 2005) and passive viewing of faces (Key & Corbett, 2014). Group differences in the topographic distribution of the observed stimulus repetition effects could be interpreted in accordance with the functional significance of the frontal vs. parietal old/new ERP effects: the decreased (more positive) FN400 response could reflect general stimulus familiarity (Curran, 2004; Friedman & Johnson, 2000), while the increased parietal positivity is associated with stimulus recall (Nessler et al., 2001; Rugg & Curran, 2007).

The presence of the parietal old/new ERP response for repeated faces but not houses in the typical group supports the idea that due to their greater salience as socially relevant stimuli, pictures of faces receive more extensive cognitive processing that could support incidental recall of the stimuli experienced during passive viewing. Conversely, in the absence of instructions directing individuals to memorize the images or detect repetitions, houses receive relatively little processing beyond basic perceptual analysis sufficient to develop familiarity with the stimulus features. Thus, both groups evidenced house repetition detection in the form of the frontal N400 response, but no parietal old/new response. Repetition-related enhancement of brain activity has been previously observed in fMRI studies in cases of increased attention to the stimuli or incidental recollection of the repeated items (see Segaert et al., 2013 for review), while passive viewing of repeated nonsocial images was associated with reduced activation of brain structures sensitive to novelty (Jessen et al., 2002).

The lack of the parietal old/new response for faces in participants with WS is surprising given reports of their increased attention to faces (Riby et al, 2011; Plesa-Skwerer et al., 2009, 2011) and interest in social interactions (Fishman et al., 2011; Mervis & Klein-Tasman, 2000). The concurrent presence of the FN400 response for repeated faces and houses suggests a possible general dissociation between familiarity and recollection processes in persons with WS. Similar findings of typical familiarity and impaired

recollection in persons with WS compared to mental-age matched controls were recently reported for nonsocial pictures (Costanzo et al., 2013).

Before considering the reasons for this possible dissociation, it is important to note high inter-individual variability in the parietal old/new response in persons with WS. Similar to the findings of Atkinson et al. (1997) who observed that only 50% of their sample of children with WS showed visual-motor deficits suggestive of dorsal visual stream deficit, in our sample, approximately 60% of the participants with WS showed some evidence of the parietal old/new response for the repeated faces. There were no obvious differences between persons with WS who did and did not show the parietal old/new effect for faces in terms of age, sex, adaptive functioning, or the early perceptual ERP responses to the stimuli. Correlational analyses also demonstrated that the parietal old/new effect in participants with WS was not related to their verbal, nonverbal, or composite IQ, replicating previous findings that ERP markers of repetition-based incidental memory are independent of intellectual functioning (Key & Dykens, 2014; Key & Corbett, 2014). Furthermore, the absence of the parietal old/new ERP effect for repeated faces in persons with WS in the 484–800 ms interval argues against the possibility of a delayed memory response due to the intellectual disability.

Persons with WS have been frequently characterized as having high rates of inattention and distractibility (e.g., Pober and Dykens 1996; Greer, Brown, et al. 1997). All participants in our study maintained their gaze on the computer screen during the task, as verified by the researcher present in the room, and they also detected the occasional probe stimuli with high accuracy. However, in the absence of explicit task-specific reasons for attending to the stimuli, neither faces nor houses might have been sufficiently salient for the individuals with WS to actively engage in extensive stimulus processing. Alternatively, it is possible that the presentation sequence in which instances of stimulus repetition were often separated by multiple novel images could exceed the capacity of memory system in persons with WS regardless of stimulus salience. Previous studies of active memory for faces in WS noted significant decrease in accuracy when interstimulus delays were longer than 2 seconds (O'Hearn et al., 2009). The latter explanation is less likely because our paradigm placed minimal demands on the participants' memory system by including a very small "memory set" (one face, one house) and a high number of repeated exposures (50 trials each) compared to 24 stimuli and 16 trials per condition used by O'Hearn et al (2009).

The neuroanatomical features of WS (see Jackowski et al. 2009 for a review) could also contribute to the observed pattern of ERP responses. Familiarity and recollection processes in recognition memory rely on distinct brain networks (Yonelinas et al., 2005; Rugg & Curran, 2007), which may directly or indirectly affect the topographic distribution of the old/new ERP responses. In particular, many aspects of attentional and memory processes depend on the fronto-parietal network (Salazar et al., 2012; Wang et al., 2010). Prior fMRI studies in persons with WS noted disproportionate reduction in grey matter in superior parietal (Eckert et al., 2006) and bilateral parieto-occipital regions (Boddaert et al., 2006). Others reported atypical connectivity of dorsal structures with the intraparietal sulcus (Meyer-Lindenberg et al., 2004), which is involved in memory retrieval (Ishai & Yago, 2006) and recognition of newly learned stimuli (Leube et al., 2003). In a typical person, the

frontal and parietal cortical regions can coordinate information processing through top-down attentional control and bottom-up target detection mechanisms (Nyberg et al., 2009; Salazar et al., 2012; Wang et al., 2010). Fronto-parietal coordination is supported by the superior longitudinal fasciculi (Tamnes et al., 2013), which shows higher than typical functional anisotropy in persons with WS (Hoeft et al., 2007), possibly due to atypical dendritic branching and reduced number of posterior parietal targets (Eckert et al., 2006).

Consequently, in persons with WS, successful performance on active memory tasks, especially those with minimal delays, may be achieved by the top-down mechanism and deliberate allocation of cognitive resources that compensate for the atypical brain organization. However, in a passive viewing task with no explicit instructions, inherent stimulus salience may not be sufficient to engage the compensatory mechanisms, making reduced coordination between brain regions more apparent.

Our exploratory analyses also revealed that variability in the old/new ERP responses could not be explained by differences in the early perceptual processing of the stimuli. Analyses of the first 200 ms after stimulus onset noted no group differences in response to faces and houses. The typical participants demonstrated enhanced right occipito-temporal responses for faces vs. houses, consistent with prior studies of the N170 response (e.g., Bentin & Duouell, 2000). Participants with WS evidenced similar perceptual discrimination in the parietal P2 response, where a larger positivity was observed for houses than faces. Interestingly, the 156–236 ms period also provided the earliest evidence of stimulus repetition detection in all participants. Repeated faces and houses were associated with larger bilateral occipito-temporal P2 and midline frontal N2 amplitudes, likely reflecting increased attention to the perceptual properties of the unexpected repetitions within a stream of novel items. Similar repetition effects independent of stimulus type (face, non-face) have been previously reported by George et al. (1997).

Although our study resulted in novel finding, it has several limitations. We did not collect any objective recollection data that could verify better memory for the repeated faces in participants whose ERPs evidenced the parietal old/new effect. The goal of our experimental paradigm was to keep the task maximally easy for participants with intellectual disability. However, in the future study, a behavioral measure of post-task identification of the repeated stimuli could provide additional information relevant to the proposed interpretation of the ERP results. Also, we did not have a specific measure of social functioning or hypersociability in participants with WS. Including such measures would strengthen future studies. We used static images, and it is possible that dynamic stimuli could facilitate memory trace development (e.g., Otsuka et al., 2009; but see O'Toole, Roark & Abdi, 2002). However, the choice of static stimuli allowed for a direct comparison of incidental memory for social (faces) and nonsocial (houses) stimuli, with the latter more typically experienced as non-moving images. Finally, our sample was not sufficiently large to fully examine the observed heterogeneity in the parietal old/new response for the repeated faces in persons with WS. Such individual differences will need to be pursued further as they may provide valuable information for understanding the WS phenotype and be relevant for educational and treatment purposes.

In sum, our results suggest that ERPs indexing incidental memory following passive exposure to social and nonsocial stimulus repetition could be an informative marker of social interest. While persons with WS may exhibit behavioral evidence of increased social interest, the ERP findings suggest that their processing of social information in the absence of specific instructions or goals can be relatively superficial. In this study, participants with WS demonstrated early perceptual differentiation of faces vs. houses, developed perceptual familiarity with both types of the repeated stimuli (evidenced by FN400), but did not show consistent evidence of greater memory for faces (lack of the significant parietal old/new response). There was also no significant difference in their detection of repeated faces vs. houses, arguing against the exceptional salience of social information in WS when it is not relevant to the task. In daily life, insufficiently extensive processing of faces could contribute to inappropriate approach behaviors that characterize WS. A stranger's face may elicit a sense of familiarity, but without the benefit of recalling the details of prior experiences with this person, individuals with WS may be unable to accurately evaluate the risks vs. benefits of approaching.

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Figure 1.
Electrode layout and the selected electrode clusters used for data analysis.

Figure 2. Averaged ERP waveforms in response to repeated and single stimuli at left and right occipito-temporal clusters for typical participants and individuals with WS.

Figure 3.
Averaged frontal old/new ERP response to repeated and single stimuli for typical participants and individuals with WS.

Figure 4. Averaged parietal old/new ERP response for repeated and single stimuli in typical participants and individuals with WS.