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Neural processing of race by individuals with Williams syndrome: Do they show the other-race effect? (And why it matters)

Inna Fishman, Rowena Ng, and Ursula Bellugi

Salk Institute, La Jolla, CA, USA

Abstract

Williams syndrome (WS) is a genetic condition with a distinctive social phenotype characterized by excessive sociability, accompanied by a relative proficiency in face recognition, despite severe deficits in visuospatial domain of cognition. This consistent phenotypic characteristic and the relative homogeneity of the WS genotype make WS a compelling human model for examining the genotype-phenotype relations, especially with respect to social behavior. Following up on a recent report suggesting that individuals with WS do not show race bias and racial stereotyping, this study was designed to investigate the neural correlates of the perception of faces from different races, in individuals with WS as compared to typically developing (TD) controls. Caucasian WS and TD participants performed a gender identification task with own-race (White) and other-race (Black) faces while event-related potentials (ERPs) were recorded. In line with previous studies with TD participants, other-race faces elicited larger amplitudes ERPs within the first 200 ms following the face onset, in WS and TD participants alike. These results suggest that, just like their TD counterparts, individuals with WS differentially processed faces of own- vs. other-race, at relatively early stages of processing, starting as early as 115 ms after the face onset. Overall, these results indicate that neural processing of faces in individuals with WS is moderated by race at early perceptual stages, calling for a reconsideration of the previous claim that they are uniquely insensitive to race.

Keywords

Williams syndrome; the other-race effect; event-related potentials; race bias

In humans, the genetic basis of sociability remains mostly inaccessible, presumably because of the subtlety of the phenotype and the pleiotropy of the implicated genes (Insel & Fernald, 2004). Williams syndrome (WS) is one of the few known examples of a subtle – and completely mapped – genetic perturbation that is associated with a substantial change in social-behavioral profile. Unlike most neurodevelopmental syndromes, WS – caused by a spontaneous hemideletion of 25–30 genes on chromosome band 7q11.23 (Ewart et al., 1993) – is characterized by *enhanced sociability*, which makes it a compelling human model for examining the biological bases of social behavior. Often referred to as “hypersociability,” this hallmark feature of the WS behavioral profile involves indiscriminate friendliness, gregariousness, a keen interest in interacting with others (particularly strangers), and loquacious and socially engaging language (Doyle, Bellugi, Korenberg, & Graham, 2004; Jarvinen-Pasley et al., 2008; Jones et al., 2000; Mervis & Klein-Tasman, 2000). The enhanced attraction to people and interest in social interactions, which are evident even

among infants and toddlers (cf. Mervis et al., 2003), are coupled with a preference for viewing, and a relatively strong skill in identifying faces (for a review, see Jarvinen-Pasley et al., 2008). In particular, despite severe deficits in visuospatial domain of cognition, individuals with WS perform at, or close to, age-appropriate level (i.e., above IQ-based expectations) on tasks involving face recognition and discrimination (Deruelle, Rondan, Mancini, & Livet, 2003; Rose et al., 2007; Tager-Flusberg, Plesa Skwerer, Faja, & Joseph, 2003; Udwin & Yule, 1991). Given that face processing is an essential aspect of most human social interactions, it has been suggested (e.g., Laing et al., 2002; Mervis et al., 2003) that the overly intense attention toward the face observed in individuals with WS may be critical to the development of their enhanced sociability (as contrasted with gaze aversion and social avoidance in autism; cf. Riby & Hancock, 2008, 2009). Overall, notwithstanding the complex cognitive and behavioral profile of WS, the unique social phenotype (i.e., excessive sociability and relative proficiency at face processing) along with a well characterized molecular genetic basis present social neuroscientists with a unique opportunity to examine core social cognition processes and their neurobiological correlates.

It is in this context that a recent study (Santos, Meyer-Lindenberg, & Deruelle, 2010) demonstrated with a simple behavioral design that individuals with WS showed no evidence of race bias. In contrast to typically developing control participants who exhibited “strong” (Santos et al., 2010, p. 307) own-race bias by assigning fewer positive associations to other-race characters as compared with own-race characters, individuals with WS attributed positive and negative features equally to both own-race (Caucasian) and other-race (non-Caucasian) experimental characters. On the other hand, both WS and control groups demonstrated a robust gender-role bias, suggesting that the absence of race bias in WS was not due to a generalized deficit in attribution abilities (nor was it due to the lower IQ, which was found to be unrelated to the task performance). The authors interpreted these results to indicate that social fear, thought to be absent in individuals with WS corollary to their hypersociability (although see Dodd, Schniering, & Porter, 2009*), but present in control individuals, contributes to development of race bias and racial stereotyping in typical development. In other words, the authors concluded that reduced social fear and hypersociability in WS could lead to an absence of racial stereotyping, which in light of the known WS genotype suggests existence of dissociable neurogenetic mechanisms for racial vs. gender biases.

Given the significance and wide-reaching implications of the argument made by Santos and colleagues, a further evidence and support for such a claim, preferably using a complementary methodology probing a different level of processing, is in order. The present study was thus designed to explore the racial bias – or the lack thereof – in WS by investigating brain activity associated with processing of faces of different races, utilizing event-related potentials (ERPs). Briefly, ERPs are derived from the ongoing electrical oscillations of the brain measured via electroencephalogram (EEG) and refer to the average electrical activity recorded in response to a specific – mental or physical – *event*. ERPs are thought to arise from the synchronous activity (namely, postsynaptic potentials) of neuronal populations engaged in processing of information at hand (cf. Fabiani, Gratton, & Federmeier, 2007). ERPs have a temporal resolution on the scale of milliseconds and are thus exceptionally sensitive to real time neural processes that unfold quickly upon perception of the face (or any other sensory input). As such, ERPs should prove useful in investigating mechanisms underlying the seeming lack of racial bias in WS because they represent a processing sequence that is upstream of the behavioral output of attribution response, which was the outcome measure in Santos et al. (2010). In other words, ERPs

*These authors, using both parent- and self-report, demonstrated that the overall level of social anxiety symptoms in WS is not unusually low.

provide information about processes that *precede* the conscious, deliberate responses measured behaviorally.

Furthermore, an additional advantage of the ERPs is that multiple components of the ERP waveform can be assessed from a single stimulus, each representing a somewhat different aspect of processing, allowing evaluation of multiple cognitive responses to the same face as they unfold in real time. Prior ERP studies focusing on processing of faces of different races (e.g., Caldara et al., 2003, 2004; He, Johnson, Dovidio, & McCarthy, 2009; Herrmann et al., 2007; Ito & Urland, 2003, 2005; Stahl, Wiese, & Schweinberger, 2008) reported differential neural activity evoked by same-race vs. other-race faces, which was observed across several ERP components. The differences emerged as early as 100 ms following the face presentation onset, captured by the P100 ERP component, with larger amplitude P100s evoked by other-race faces (He et al., 2009; but see Vizioli, Foreman, Rousselet, & Caldara, 2010). The P100 is a positive deflection detected at occipital sites that peaks at around 100–130 ms post-stimulus. While it is thought to reflect processing of the low-level features of stimuli, its sensitivity to race suggests that race-related cues are available remarkably early in face processing, before more fine-grained perceptual processes are complete.

Two other components, the P200 and N200 that peak, respectively, at ~160 ms and ~250 ms over frontal-central scalp sites, have been consistently associated with race-related differences in face processing, such that other-race faces appear to elicit enhanced P200 amplitudes, while same-race faces elicit larger N200 amplitudes (e.g., Dickter & Bartholow, 2007; He et al., 2009; Ito & Urland, 2003, 2005; Willadsen-Jensen & Ito, 2006; but see Stahl et al., 2008 and Vizioli et al., 2010, for different results). Both P200 and N200 have been related to the active categorization of visual stimuli, and their sequential relationship (the P200 preceding in time the N200) suggests that attention is initially captured by other-race faces and is then redirected to the same-race faces.

Naturally, the effect of race has also been assessed with the face-preferential N170 component considered to be an index of the configural processing of faces due to its robust differential response to faces vs. any other non-face visual objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bentin & Deouell, 2000; Itier & Taylor, 2004). The N170 is a negative deflection detected at the lateral occipito-temporal scalp sites that peaks around 170 ms post-stimulus and tends to be larger over the right hemisphere (Bentin et al., 1996). Evidence from source localization studies suggests that the N170 is generated in the fusiform gyrus (or the fusiform face area, FFA) and the superior temporal sulcus (STS; Itier & Taylor, 2004; Kanwisher, McDermott, & Chun, 1997). Notably, the evidence regarding whether the N170 is sensitive to race has been, thus far, surprisingly inconsistent (in part due to differences in tasks used to elicit the N170; e.g., direct race categorization vs. gender identification). While some studies reported no race effect on the N170 using a passive face viewing paradigm (Caldara et al., 2003), an active race classification task (Caldara et al., 2004), an old-new face recognition task (Tanaka & Pierce, 2009), or an oddball face task (Vizioli et al., 2010), others found an enhanced N170 to same-race faces (using an active race classification task; Ito & Urland, 2005), while yet others reported larger N170s to other-race faces using a priming task (Herrmann et al., 2007) or a passive face viewing task (Stahl et al., 2008; Walker, Silvert, Hewstone & Nobre, 2008). Despite the multiplicity of outcomes, it appears that at least under certain conditions the N170 is implicated in race processing, alongside the initial configural face encoding.

Given the above evidence that race captures attention very early in neural processing, as demonstrated by its effect on the ERP components elicited within the 250 ms from a face onset, the present study was designed to examine whether individuals with WS and typically developing (TD) controls exhibit comparable sensitivity to race, as measured by ERP

responses to same- vs. other-race faces. To this end, neural responses to an unrelated gender categorization task were measured in order to investigate whether, and to what extent, attention was spontaneously drawn to race, in WS and TD participants, even when race was irrelevant to the task-specific goals. Gender categorization paradigms have been successfully used with ERP measures to examine implicit race processing in TD individuals (e.g., Dickter & Bartholow, 2007; He et al., 2009). Further, the ERPs allow measuring the processes that unfold quickly upon perception of faces (or any other stimuli). Thus, this investigation was designed to supplement the behavioral results of Santos et al. (2010) with psychophysiological measures such as ERPs, which represent neural activity transpiring upstream of – and thus uncontaminated by – the conscious categorization decisions used as an outcome measure by Santos and colleagues. The ERP components previously implicated in the perception of race, as reviewed above – namely, the P100, N170, P200, and N200 – were targeted. Based on the prevalent account maintaining that individuals with WS demonstrate enhanced attention to (and greater fixation on) faces (cf. Riby & Hancock, 2008, 2009) – which might explain their hypersociability – one would expect no ERP differences based on the target face race in WS individuals, due to their presumed engrossment with the face as a whole. Alternatively, given the same premise of the enhanced attention to faces in WS, one might reason that individuals with WS should demonstrate ERP race effects precisely because of the greater attention – and, correspondingly, greater neural processing (cf. Golarai et al., 2010) – that they allocate to social stimuli such as faces. Given that no prior studies have focused on race perception in WS at the level of brain processing, no particular outcome was favored a priori.

Method

Participants

Sixteen individuals diagnosed with WS (8 males; mean age 27 ± 5.6 years, range 20–38 years) were recruited nationally and from the local community as part of an ongoing multicenter research program focused on investigating the neurogenetic mechanisms of the WS phenotype. The genetic diagnosis of WS was based on fluorescent *in situ* hybridization probes for elastin, a gene consistently found to be deleted in WS (Ewart et al., 1993). All participants with WS had typical deletions and exhibited the clinical phenotype associated with this condition (Korenberg et al., 2000). Fifteen healthy individuals (8 males; mean age 23 ± 5.6 years, range 19–40 years) were recruited through advertisements in local newspapers and fliers posted in the community and constituted the TD control group. All TD participants were screened for the level of education, and only those with no more than two years of college-level education were included in the study. TD participants were screened to rule out history of central nervous system (CNS) disorder or injury, current or past psychiatric conditions, and current use of medications affecting CNS.

All participants were Caucasian Americans, drawn from a larger pool of multiracial American individuals participating in the ongoing research program described above. Demographic and psychometric information for each group is summarized in Table 1.

Stimuli

Thirty color headshots of faces with neutral facial expression from 30 unique individuals were used (NimStim Face Stimulus Set; Tottenham et al., 2009). These included 15 White and 15 Black faces (half male and half female). In two blocks, faces drawn from this set were presented pseudo-randomly, with one gender appearing on 80% of the trials (e.g., male) and the other (e.g., female) appearing on 20% of the trials (gender was counterbalanced between the blocks, and the order was counterbalanced between participants). A pseudo-random presentation was constrained by two additional parameters:

(a) the same stimulus was not to be presented on two consecutive trials, to avoid potential sequential effects on ERPs; (b) the stimuli were drawn from the available images in a manner assuring an equal number of faces from each race. Participants were instructed to categorize the face gender by pressing one of two designated keys (counterbalanced across participants).

Procedure

ERP task—Participants viewed a series of faces (pseudo-randomly drawn from the 30 available images) presented one at a time, in two blocks of 60 trials each. Each trial consisted of a 500-ms presentation of a fixation cross, followed by an 800-ms presentation of a face, to which ERPs were time-locked, with an intra-stimulus-interval (ISI) of 1000 ms. To obscure the true purpose of the study, participants were asked to classify the face as male or female by pressing a key corresponding to their choice. The two blocks were separated by a self-paced break, constrained to last no less than 1 minute. Stimulus delivery and the recording of overt responses were controlled by E-Prime 2.0 (Psychology Software Tools (PST), Inc.; Pittsburgh, PA), in combination with the PST serial response box.

Participants were first exposed to 10 practice trials, during which verbal feedback was provided, to ensure that the participants, especially those with WS, understood the instructions and the task at hand. Behavioral and electrophysiological responses to these practice stimuli were not included in later analyses. Behavioral data, namely, accuracy (percent of correct responses) and response times (RTs), were recorded by the E-Prime software.

Cognitive Testing—In a separate session, participants were administered a battery of standardized cognitive tests, in order to ascertain the average range of cognitive abilities in each group, which can potentially confound the interpretation of ERP outcome variables. As a measure of general cognitive ability, all participants were administered the Wechsler Adult Intelligence Scale Third Edition (WAIS-III; Wechsler, 1997) from which verbal, performance and overall intelligence quotients (VIQ, PIQ and FSIQ) were derived. The IQ scores achieved by each group are displayed in Table 1. A repeated measures ANOVA between the groups revealed a significant main effect of group ($F(2, 43) = 34.9, p < .001$), such that the TD group obtained significantly higher scores on VIQ, PIQ and FSIQ than the WS group (all $ps < .01$), as was expected given the well-documented cognitive phenotype of WS.

EEG recording, off-line processing, ERP component extraction and analysis—

EEG data were recorded using NetStation 4.0 (Electrical Geodesics, Inc.; EGI, Eugene, OR), with a 64-channel Geodesic Sensor Net with Ag/AgCl electrodes. The EEG data were acquired continuously at a sampling rate of 250 Hz (i.e., sampled every 4 ms) and filtered offline with a 0.1 to 40 Hz bandpass filter. The filtered data were segmented into epochs starting 100 ms before stimulus onset and extending to 900 ms after stimulus onset, subjected to automated artifact detection (removal of epochs containing voltage deflections of $\pm 70 \mu V$ in any one of the channels), corrected for vertical and horizontal eye movements (Gratton, Coles, & Donchin, 1983), re-referenced to average reference, and baseline-corrected using the average of the 100-ms pre-stimulus epoch. The resulting 1000-ms-long epochs were then averaged separately by category (stimulus gender, stimulus race) generating four separate average waveforms (males, females, Black, White) for each participant. The amplitudes of the target ERP components (described in the Introduction) for each participant were quantified as the largest (positive, for P100 and P200, or negative, for N170 and N200) voltage over a time window beginning 25 ms before, to 25 ms after the group-average peak latency. The means of these amplitudes were analyzed using repeated

measures analysis of variance (ANOVA) with group (WS, TD) as the between-subjects variable and the stimulus race (Black, White) and gender (male, female) as the within-subjects variables. The primary objective of these comparisons was two-fold: assessing whether there was a differential attention to race (a task-irrelevant dimension) in comparison to gender, and whether the effect of race was comparable for WS vs. TD participants. Greenhouse–Geisser correction was applied to p values in all analyses involving multiple numerator degrees of freedom. For current purposes, analyses of each component of interest were restricted to the electrode at which they were maximal (as determined by the NetStation software using each group grand-average waveforms). Finally, a series of correlation analyses using Pearson's correlation was conducted to determine the influence of IQ on the amplitude of the ERP components.

Results

Behavioral performance on gender identification task

First, response times (RTs) from the gender categorization task were sorted according to their correctness and only correct-trial RTs were included in the analyses. Further, only RTs that fell within ± 3 SD from each group mean were included, which resulted in excluding between 1 to 11 responses (out of 120 trials, or less than 10%) in 6 participants with WS from the analyses of behavioral responses. Analyses of RTs revealed that latency of deciding whether the person was a man or a woman significantly differed for faces from different races. Specifically, a 2 (Race: Black, White) $\times$ 2 (Group: WS, TD) repeated measures ANOVA revealed a main effect of race, namely, that both WS and TD participants had faster responses (lower RTs) when responding to Black ($M = 539$ ms) than to White faces ($M = 562$ ms; $F(1, 29) = 13.10$, $p = .001$, $\eta_p^2 = .34$). This result is consistent with prior studies reporting faster performance on categorization of other-race faces (e.g., Caldara et al., 2004). There was also a significant group effect, in that participants with WS had overall slower responses (greater RTs: $M = 650$ ms) than the TD participants ($M = 450$ ms; $F(1, 29) = 12.08$, $p = .002$, $\eta_p^2 = .32$), which is line with previous reports on response latency in WS (e.g., Mobbs, Garrett, Menon, Bellugi, & Reiss, 2004).

Next, analysis of accuracy revealed that, overall, participants were highly accurate at judging the gender of faces, indicating that they remained alert and attentive throughout the task. A 2 (Race: Black, White) $\times$ 2 (Group: WS, TD) repeated measures ANOVA revealed no significant effects as a function of race or group: Participants were as accurate in judging the gender of Black faces (97%) as they were in judging the gender of White faces (96%; $F(1, 29) = 1.40$, $p > .05$), and the WS group's accuracy (95%) was not significantly different from that of the TD group (98%; $F(1, 29) = 3.34$, $p > .05$).

ERPs

The following ERP components were measured because prior research has found them to be sensitive to race of the stimuli faces, as reviewed in the Introduction: P100, N170, P200, and N200. The findings pertaining to these components will be discussed below in temporal sequence. Initial analyses were performed by the NetStation software to determine scalp locations (across all participants) where these components of interest were maximal. Figure 1 represents the ERP waveforms at these maxima locations.

P100—The bottom panel of Figure 1 represents the ERP waveforms at the occipital Oz electrode (where the P100 is typically observed), averaged separately for Black and White target faces. The P100 can be seen as a positive deflection with a peak latency of ~ 115 ms following the face onset. A repeated measures ANOVA revealed a main effect of race ($F(1, 29) = 7.27$, $p < .01$, $\eta_p^2 = .22$), such that the P100 amplitudes evoked by Black faces ($M =$

5.56 μV) were larger than those elicited by White faces ($M = 4.95 \mu\text{V}$). There were no other significant main effects (face gender, or group) or interaction effects (all p s > .25).

N170—Figure 1, middle panel, shows an N170 component, a negative deflection with a peak latency of ~ 175 ms over the right occipito-temporal electrode site, averaged separately for faces of different race. A repeated measures ANOVA revealed a main effect of race ($F(1, 29) = 7.50, p < .01, \eta_p^2 = .22$), such that the amplitude of the N170 elicited by Black faces ($M = -7.26 \mu\text{V}$) was significantly larger than that elicited by White faces ($M = -6.54 \mu\text{V}$). No significant N170 amplitude differences were found between groups ($p = .22$), or for faces of different gender ($p = .86$).

P200—Figure 1, top panel shows the average ERPs elicited by faces of different races at the fronto-central electrode, Fz, where the P200 is typically at its maximum. The P200 can be seen as a positive deflection peaking at ~ 190 ms following the face onset. Once more, a main effect of race was observed ($F(1, 29) = 15.42, p < .001, \eta_p^2 = .36$), with Black faces eliciting larger P200 amplitudes ($M = 5.50 \mu\text{V}$) than White faces ($M = 4.73 \mu\text{V}$). There were no other significant P200 amplitude differences between groups ($p = .08$), or for faces of different gender ($p = .79$).

N200—An N200 was observed with maximal amplitude at the fronto-central electrode, Fz, and a peak latency of ~ 250 ms, as shown in Figure 1, top panel. There was no significant N200 amplitude difference between Black and White faces ($F(1, 29) = 3.71, p = .07$), with Black faces eliciting comparable N200 amplitude ($M = -6.50 \mu\text{V}$) in comparison to White faces ($M = -7.05 \mu\text{V}$). There was a significant group effect ($F(1, 29) = 6.14, p < .01, \eta_p^2 = .21$), such that, overall, the WS group had larger N200 amplitude ($M = -8.47 \mu\text{V}$) than the TD group ($M = -4.76 \mu\text{V}$). No significant N200 amplitude differences between the faces of different gender were found, and there were no significant interactions effects.

Finally, correlation analyses (Pearson r tests) computed for each group separately failed to reveal any significant correlation between IQ indices and the other- vs. same-race difference scores calculated for all four ERP components, for both WS (all p values > .15) and control (all p values > .23) groups, suggesting that cognitive abilities did not account for the race effects found in both groups.

Discussion

The goal of the present study was to explore how own- vs. other-race faces are processed in the brains of individuals with WS, relative to TD controls, as reflected by ERP components evoked by faces. This comparison was motivated by a recent finding reported by Santos and colleagues (2010) suggesting that, unlike their TD counterparts, individuals with WS showed no race bias on a behavioral measure of racial attitudes. To investigate this phenomenon at the level of brain processing, ERP components elicited by faces of different races were measured in participants with WS and chronological-age-matched TD controls, using a gender categorization oddball task (utilized in the past to measure the other-race ERP effects in TD individuals), in which gender and race served as the task-relevant and the task-irrelevant dimensions, respectively.

The study's main finding was that *all* the study participants – with and without WS – differentially processed faces of own- vs. other-race, at relatively early stages of processing. Significant race effects emerged in three out of four ERP components identified by prior research to be implicated in processing of race, starting as early as 115 ms after the face onset. Namely, race systematically modulated the amplitudes of the P100, N170, and P200, such that other-race faces elicited larger amplitudes on these components, in TD and WS

participants alike. Importantly, the race effects emerged despite the fact that race was a task-irrelevant dimension. These data suggest that, just like TD controls, individuals with WS spontaneously classify faces on racial dimension. On the other hand, no significant gender effects were found for any of the four ERP components, suggesting that overt processing goals (i.e., gender categorization) had little effect on the category to which both WS and TD individuals attended at these early stages of processing.

Crucially, there were no significant group by race interaction effects, indicating that race had similar effects on neural processing of faces in both WS and TD groups. That is, the difference between the ERPs evoked by other- vs. own-race faces was the same polarity and overall magnitude across *all* participants, with larger ERP amplitudes (for the P100, N170 and P200 components) elicited by other-race target faces. This signifies that, despite the prevailing assertion that face stimuli might be inherently more meaningful for individuals with WS than for TD controls, both groups “attended” to race in a similar manner (despite its irrelevance to the task). This conclusion is further supported by the behavioral (response latency) data, which demonstrated that categorizing face by gender was faster for faces of other race, in both WS and TD groups.* Thus, the RT patterns also suggested that *all* participants, with or without WS, had a difficult time controlling their automatic orienting toward racial information, even though doing so would have been beneficial to their performance on the task at hand.

To the extent that one can compare data across different levels of processing, these results are contrary to the conclusion that Santos and colleagues reached based on their behavioral racial attitudes data. In their study individuals with WS showed no racial bias (i.e., there was no effect of race in WS group) when asked to match characters of different races to positive or negative narratives about these characters. In contrast, the current data present evidence of race effect in WS at the level of non-deliberate, automatic brain processing, which occurs very early in the processing sequence and precedes, chronologically, the conscious, deliberate choices quantifiable by behavioral attitude scales such as the one used by Santos and co-authors. Given the speed and the automaticity of the processes measured by the early ERP components targeted in the present study, these findings implicate that individuals with WS show evidence of as much implicit* “race bias” as their age-matched TD counterparts do.

While remaining mindful of the many methodological differences between the current study and the one by Santos and colleagues (participants’ age: young adults vs. children and adolescents; stimuli: photographs of faces vs. drawings of full-body characters; outcome measures: indices of neural processing vs. behavioral attitudes, correspondingly), we underscore the fact that, to our knowledge, these are the only two extant studies addressing the question of race processing in WS – and demonstrating conflicting results. Importance of this topic stems from the assertion put forward by Santos and colleagues that WS might be the only “human group...[characterized by] the absence of racial stereotyping” (p. 307). Given this grand contention, the apparent inconsistency between the present and Santos et al.’s findings and conclusions should be resolved with future studies.

*In addition to the main effect of race, a main effect of group was found indicating overall slower responses in WS than in TD participants. Of interest, this latter finding of discrepant behavioral performance in TD and WS groups despite an absence of ERP group effects is reminiscent of other studies in WS that found a discrepancy between behavioral performance on tasks involving processing of socially relevant information, such as faces, and neural (ERP and/or fMRI) outcomes (Mills et al., 2000; Haas et al., 2009).

*Arguably, processes measured by ERPs qualify as an instance of implicit processing by almost any definition available: they operate outside awareness, are non-effortful and are influenced by prior learning without the individual’s deliberate recollection of this learning, etc.

How do these results fit what is known about the WS phenotype?

Overall, these results indicate that neural processing of faces in individuals with WS is genuinely sensitive to the face race. Just like in TD individuals, the neural face system in WS is responsive to race at early perceptual stages of processing, as demonstrated by systematic modulation of the amplitudes of the P100, N170, and P200 ERP components. Whether this sensitivity to race at this early, automatic stages of information processing has implications for behavior of individuals with WS is unclear, although the current response latency data suggest that, similarly to the TD peers, WS individuals make ingroup-outgroup distinctions when asked to categorize target faces on an unrelated dimension such as gender. Of course, these findings do not necessarily tell us if and how this other-race effect observed at both psychometric and neural levels in WS may manifest in real social contexts.*

Based on the behavioral evidence that individuals with WS are less reserved towards strangers (Gosch & Pankau, 1994), it has been suggested that they are unable to detect social danger signals (Meyer-Lindenberg, Mervis, & Berman, 2006). Lending support to this notion, some recent studies reported that, as compared with controls, those with WS exhibit attenuated amygdala response to threatening faces (Haas et al., 2009; Meyer-Lindenberg et al., 2005) and are less able to perceive negatively valenced emotional facial and vocal expressions (Plesa-Skwerer, Faja, Schofield, Verbalis, & Tager-Flusberg, 2006). If other-race faces signal social threat – as is suggested by Santos et al. (2010) – then current results call for reconsideration of this view, as they implicate that individuals with WS, in fact, “perceive” those signals, at least at the very early stage of information processing, just as their TD counterparts do. In other words, these results demonstrate remarkable “normalcy” of the way their brains process incoming stimuli potentially signaling social threat, at least early (in the first 200 ms) in the information processing stream. In fact, the remarkable similarity of the ERP findings in WS and TD participants parallels an fMRI result suggesting a relative integrity (i.e., similar to TD controls BOLD activation levels) of the face processing pathways, including the fusiform gyrus, superior temporal sulcus and amygdala, while viewing faces with neutral expressions (Mobbs et al., 2004; although WS participants also showed additional widespread activation in the right inferior, superior, and medial frontal gyri, anterior cingulate, and several subcortical regions encompassing the anterior thalamus and caudate).

Overall, the WS hallmark behavioral feature of hypersociability does not readily account for the current results. Namely, the hypersociability framework would suggest that individuals with WS might “ignore” the skin color, with the social status of the face stimuli having a greater impact than the face race (or any other face feature). However, the significant race effects on the early ERP components and the absence of group effects both suggest that WS individuals, similarly to TD controls, did not “overlook” the race of the faces, at least at the preattentive, automatic level of face processing. It is entirely possible, of course, that still photographs of faces used as stimuli in the present study are not as rewarding and engaging as a live human interaction, and therefore the reputed increased social drive attributed to individuals with WS did not affect the early processing of faces within the 200 ms following the face onset.

Further, from the developmental point of view, there is a large body of evidence suggesting that the sensitivity to race (as manifested in other-race faces being detected more readily and classified more rapidly than own-race faces) can be first detected, with visual preference

*There is some evidence, from research with TD individuals, suggesting a link between electrocortical sensitivity to race and application of activated racial stereotypes, such that participants who exhibit greater P200 and N200 differentiation between own- and other-race target faces show more pronounced behavioral racial bias when forced to respond to the other-race armed targets (Correll, Urland, & Ito, 2006).

methodology, as early as 3 months of age (see Kelly et al., 2009, for a review). Thus, given the neurodevelopmental nature of WS, future research should examine when this ability is first manifested or begins to emerge in infants with WS. It remains possible, and even likely, that children with WS might develop the evidently universal sensitivity to race at a later stage. A challenge for future research will be to examine when the other-race effect emerges in WS, both with brain imaging and behavioral paradigms.

Current results in a larger context of the ERP race effects literature

The current data also add to a growing body of evidence that social factors such as race can influence early stages of perceptual processing of faces, at a neural level. The ERP components targeted by this investigation have been identified in prior research with TD samples as implicated in race processing; following is a brief review of the results pertaining to each of these components. First, the present data replicated previous findings (He et al., 2009) indicating that other-race faces evoked a larger P100 measured over occipital scalp sites, as compared with same-race faces, when participants performed a task in which the race of the face was irrelevant. Given that the earliest neural activity evoked by any visual stimulus occurs in primary visual cortex at around 70–80 ms after the stimulus onset (as recorded on scalp; Jeffreys & Axford, 1972), the P100 race effect found in the current data highlights that race-related configural cues are available very early in neural processing, both in TD and WS participants. While it is plausible that the effect of race on the P100 reflects differences between featural (lower-level) visual properties of the faces of two races (e.g., skin tone affecting luminance and contrast), which are known to modulate early ERP components (e.g., Hillyard, Teder-Salejari, & Munte, 1998), there is also evidence that the P100 is modulated by facial expression (Batty & Taylor, 2003; Eger, Jedynak, Iwaki, & Skrandies, 2003), which – similarly to race – represents an instance of salient information rapidly extracted before more fine-grained perceptual processing is complete. Notwithstanding the mechanisms underlying the effect of race on the P100, the current results indicated that race modulated the amplitude of the P100 in both TD and WS participants, consistent with previous findings in TD individuals (He et al., 2009).

Secondly, as reviewed above, studies exploring race effect on the N170 amplitude in TD samples have yielded highly inconsistent results, spanning from no effect to the enhanced N170 in response to either other- or own-race faces (as reviewed in Ito & Bartholow, 2009). Hence, inevitably, the present finding of the increased N170 amplitudes elicited by other-race target faces (in both WS and TD groups) is consistent with at least some of the reported data (He et al., 2009; Herrmann et al., 2007; Stahl et al., 2008; Walker et al., 2008). The N170 is considered to be an index of the structural, or configural encoding of the face (Bentin et al., 1996; although later research suggests that it may reflect more advanced stages of face processing, given its sensitivity to facial expression; see Batty & Taylor, 2003) and is the earliest neural indicator that a face is detected. Thus, the finding that race modulates the N170 amplitude suggests that race is perceived as soon as the brain recognizes a face as such, in WS and TD participants alike.

Finally, the observed race effect on the P200 (i.e., larger P200 amplitudes were elicited by other-race faces) was also in agreement with most previous findings in TD (Dickter & Bartholow, 2007; He et al., 2009; Ito & Urland, 2003, 2005; Willadsen-Jensen & Ito, 2006). Given the general sensitivity of the P200 to attentional and categorization processes (cf. Fabiani, Gratton, & Federmeier, 2007), these results reflect that both WS and TD participants encoded and oriented toward racial information. The absence of the N200 race effect, however, was inconsistent with prior studies reporting larger N200s in response to own-race faces (e.g., Dickter & Bartholow, 2007; Ito & Urland, 2003, 2005; Kubota & Ito, 2007; Willadsen-Jensen & Ito, 2006, 2008). It is possible that this absent N200 race effect was overshadowed by the main effect of group on the N200 amplitude, such that individuals

with WS demonstrated overall larger N200 amplitudes than TD controls (which appears to be a characteristic feature of individuals with WS, as demonstrated in a large WS sample by Mills et al., 2000). Altogether, the N200 component notwithstanding, the current findings are in agreement with most recent research demonstrating the continued effects of race over consecutive stages of face processing within the first 200 ms from face onset.

Conclusion

The data reported here provide evidence that, just like their TD peers, individuals with WS process faces of other race differentially than faces of their own race, as evident by distinct brainwaves as early as 100 to 200 ms following face onset. Future research should address whether the pattern of results obtained with Caucasian individuals can be extended to WS individuals of other races (it has already been shown to hold in TD samples representing different racial groups), using a full cross-over design between the races of participants and the race of the faces used as experimental stimuli, and how early in the lifespan can this sensitivity to race be first detected in WS individuals. Overall, these findings do not support the claim that people with WS microdeletion are uniquely insensitive to race, at least as regards the instantaneous neural processing of this potent social category.

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Figure 1. Group-averaged ERP waveforms recorded at Fz (the frontal midline electrode; top panel), PO8 (the lateral temporo-occipital electrode; middle panel) and Oz (the central occipital electrode; bottom panel) in response to Black and White faces. Zero time marks stimulus onset. Positive voltages are plotted as downward deflections.

Table 1

Demographic and psychometric data for WS and TD groups

Group	Gender		Age	IQ:			Verbal <i>M</i> (SD)	Performance <i>M</i> (SD)
	N	F/M		<i>M</i> (SD; range)	Full Scale <i>M</i> (SD)			
WS	16	8/8		27 (5.6; 20–38)	68 (6.4)		72 (6.1)	67 (7.4)
TD	15	7/8		23 (5.6; 19–40)	100 (11.8)		101 (11.0)	100 (11.2)

Note. The WS group had significantly lower IQ indices than the TD group (all *ps* < .001).