

# Intact Recognition, but Attenuated Adaptation, for Biological Motion in Youth with Autism Spectrum Disorder

Jeroen J. A. van Boxtel, Mirella Dapretto, and Hongjing Lu

Given the ecological importance of biological motion and its relevance to social cognition, considerable effort has been devoted over the past decade to studying biological motion perception in autism. However, previous studies have asked observers to detect or recognize briefly presented human actions placed in isolation, without spatial or temporal context. Research on typical populations has shown the influence of temporal context in biological motion perception: prolonged exposure to one action gives rise to an aftereffect that biases perception of a subsequently displayed action. Whether people with autism spectrum disorders (ASD) show such adaptation effects for biological motion stimuli remains unknown. To address this question, this study examined how well youth with ASD recognize ambiguous actions and adapt to recently-observed actions. Compared to typically-developing (TD) controls, youth with ASD showed no differences in perceptual boundaries between actions categories, indicating intact ability in recognizing actions. However, children with ASD showed weakened adaptation to biological motion. It is unlikely that the reduced action adaptability in autism was due to delayed developmental trajectory, as older children with ASD showed weaker adaptation to actions than younger children with ASD. Our results further suggest that high-level (i.e., action) processing weakens with age for children with ASD, but this change may be accompanied by a potentially compensatory mechanism based on more involvement of low-level (i.e., motion) processing. *Autism Res* 2016, 00: 000–000. © 2016 International Society for Autism Research, Wiley Periodicals, Inc.

**Keywords:** biological motion; autism spectrum disorder; adaptation; context; global processing; local processing

## Introduction

The ability to perceive and interpret other people's actions is crucial for survival in a social environment. Human newborns already show a selective preference for motion patterns generated by other living organisms—biological motion [Simion, Regolin, & Bulf, 2008]. This evolutionarily basic ability can be impaired in people with autism spectrum disorder (ASD) [Blake, Turner, Smoski, Pozdol, & Stone, 2003; Klin, Lin, Gorindo, Ramsay, & Jones, 2009], which likely contributes to the cognitive and social consequences of autism in later life [Frith, 1989; Kaiser & Shiffrar, 2009]. Hence, it has been suggested that deficits in biological motion perception may represent a hallmark feature of ASD [Pavlova, 2012].

The literature provides mixed results regarding which mechanisms underlying biological motion processing are affected in ASD. It has been consistently reported that people with ASD are less capable of extracting emotional content from biological motion displays

[Hubert et al., 2007; Moore, Hobson, & Lee, 1997; Nackaerts et al., 2012; Parron et al., 2008]. However, there is conflicting evidence regarding the impact of ASD on basic biological motion perception tasks, such as action detection tasks (e.g., detecting an action embedded in background noise) and action discrimination tasks (e.g., discriminating a walker from a runner), with some reports suggesting an impairment [e.g., Annaz et al., 2010; Blake et al., 2003; Klin et al., 2009; Koldewyn, Whitney, & Rivera, 2010; Nackaerts et al., 2012], and others not [Cusack, Williams, & Neri, 2015; Jones et al., 2011; Murphy, Brady, Fitzgerald, & Troje, 2009; Saygin, Cook, & Blakemore, 2010].

At least three potential factors may contribute to this observed variability in action detection and discrimination in ASD. First, studies of biological motion perception in ASD have used different age ranges. Many studies reported the absence of a deficit in biological motion detection/discrimination tasks when testing older participants [Murphy et al., 2009; reviewed in Kaiser & Pelphrey, 2012], suggesting that the impairments

From the School of Psychological Sciences, Faculty of Medicine, Nursing and Health Sciences, Monash University, Clayton, Australia (J.J.A.v.B.); Department of Psychiatry and Biobehavioral Sciences, Ahmanson-Lovelace Brain Mapping Center, University of California, Los Angeles, Los Angeles (M.D.); Department of Psychology and Statistics, University of California, Los Angeles, Los Angeles (H.L.); Department of Statistics, University of California, Los Angeles (H.L.)

Received July 23, 2015; accepted for publication November 27, 2015

Address for correspondence and reprints: Jeroen J.A. van Boxtel, School of Psychological Sciences, Faculty of Medicine, Nursing and Health Sciences, Monash University, Clayton, Australia. E-mail: j.j.a.vanboxtel@gmail.com

Published online 00 Month 2015 in Wiley Online Library (wileyonlinelibrary.com)

DOI: 10.1002/aur.1595

© 2016 International Society for Autism Research, Wiley Periodicals, Inc.

in biological motion processing found in children with ASD may be attenuated in adulthood. This age-related change may be due to a delayed developmental trajectory in ASD, or the emergence of potentially compensatory mechanisms in adult samples.

Second, studies may have probed different levels of hierarchical processing for biological motion perception. During the perception of human activity as portrayed in point-light animations [Johansson, 1973], individual joints move along separate trajectories. This local information must be integrated into a global percept of body posture changes, which constitute an action. Biological motion perception is thus a prime example of hierarchical processing. Numerous studies with typically-developing (TD) participants have shown that the biological motion processing system uses dual processes: one specialized for detecting local joint movements using general motion detectors [e.g., motion profiles of certain joints; Casile & Giese, 2005; Troje & Westhoff, 2006; van Boxtel & Lu, 2012, 2015], and another specialized for identifying posture changes in a holistic and global manner [e.g., bodily movements; Lange & Lappe, 2006; Lu, 2010; Thurman & Lu, 2013]. Therefore, the impact of ASD on any potential deficit at a global action processing stage may be enhanced or camouflaged by the propagation of processing differences at a local level. Previous research has indeed reported local motion processing differences between ASD and TD [Dakin & Frith, 2005; Simmons et al., 2009]. For example, research on the perception of second-order (i.e., contrast-based) motion tasks, suggested that people with ASD perform worse than neurotypical controls [Bertone, Mottron, Jelenic, & Faubert, 2003]. A similar deficit has been reported for coherent motion perception [Simmons et al., 2009], although not when controlling for intelligence quotient (IQ) [Koldewyn, Whitney, & Rivera, 2010]. The relative involvement of local and global processes likely depends on specific tasks and stimuli, which may explain the discordant findings regarding biological motion perception in ASD [see e.g., Koldewyn, Jiang, Weigelt, & Kanwisher, 2013; Milne & Szczerbinski, 2009; Simmons et al., 2009; Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015].

Third, the perception of biological motion depends strongly on both its spatial context (what surrounds a given action) and its temporal context (what actions have been observed in the recent past). Most previous research concerning ASD studied detection or discrimination of human actions in displays devoid of any spatial and temporal context. This article aims to address this gap by investigating the contextual effects in the temporal dimension: how preceding actions bias perception of currently observed actions. Such contextual processing in the temporal domain reflects one form of

adaptability of the human visual system. Action adaptability is useful in everyday life to detect small changes in observed action sequence: Imagine a person approaching you with a slow walk. Your visual system adapts to the walking action resulting in enhanced sensitivity to other actions (e.g., perceive the action more readily as running when the person suddenly increases the walking speed). In laboratory tests, research on typical populations has shown that prolonged exposure to one action gives rise to an aftereffect that biases the perception of a subsequently displayed action in terms of actor gender [Troje, Sadr, Geyer, & Nakayama, 2006] and action category [de la Rosa, Streuber, Giese, Bulthoff, & Curio, 2014; van Boxtel & Lu, 2013b]. Whether people with ASD show such adaptation effects for biological motion stimuli remains unknown.

To investigate the impact of ASD on adaptation-induced changes at different processing levels, we used psychophysical adaptation paradigms [Kovacs, Cziraki, Vidnyanszky, Schweinberger, & Greenlee, 2008; van Boxtel, Alais, & van Ee, 2008; van Boxtel & Lu, 2013b]. Adaptation techniques have been referred as the “psychophysicist’s microelectrode” [Frisby, 1979] with which one can examine hierarchical processing at different levels [Kohn & Movshon, 2004; Lee & Lu, 2012]. Local processing refers to the processing of simple visual features (e.g., orientation, motion trajectory) that is performed in early visual cortical areas, with neurons that have small, location-specific, receptive fields. Global processing refers to the analysis of complex objects as a whole (e.g., objects, faces, actions), which is performed in higher areas within the cortical stream that are usually location-invariant [Dakin et al., 2005]. Because of this link between low-level with local processing (and high-level with global processing), we will use these terms interchangeably in this article. We displayed a test stimulus at the same or a different location from the adapting stimulus. Testing at different locations can reveal position-invariant, high-level adaptation effects induced in the action-sensitive area [Grossman, Jardine, & Pyles, 2010]. By contrast, testing at the same location makes it possible to detect position-specific, low-level motion adaptation effects [Knapen, Rolfs, & Cavanagh, 2009] induced at early motion-sensitive areas such as V1 and MT. Hence, this paradigm allows us to gauge both local and global processing in ASD.

In this study, we examine all three potential sources of variability among previous research on biological motion perception in ASD. First, we compared individuals with ASD and neurotypical controls during both action discrimination and action adaptation tasks, thereby examining the impact of temporal contextual processing on action recognition in ASD. Second, we recruited individuals in late childhood and adolescence,

**Table 1. Participant Information**

Measure	TD group ( <i>n</i> =17)		ASD group ( <i>n</i> = 16)		<i>t</i> statistics	<i>P</i> -value
	Mean (SD)	Range	Mean (SD)	Range		
Age	13.32 (3.53)	8.07–17.49	14.04 (2.24)	8.25–17.58	0.66	0.51
Performance IQ	108.59 (12.37)	89–138	99.94 (15.92)	79–145	1.70	0.10
Verbal IQ	113.71 (15.55)	89–151	104.12 (19.74)	80–155	1.51	0.14
Full-score IQ	112.24 (14.01)	90–141	101.50 (20.14)	75–156	1.73	0.09
ADOS severity score	–	–	8.06 (1.20)	6–10	–	–
ADOS (social)	–	–	10.88 (2.00)	7–15	–	–
ADOS (repetitive beh.)	–	–	3.12 (1.73)	0–6	–	–
ADOS (total)	–	–	14.00 (2.81)	9–19	–	–

to cover the age-range in which changes in social perception are likely to take place. Based on the literature discussed above, we expected to find age-related change for action-specific processing only in the ASD group. Last, we tested both location-specific and location-invariant adaptation to investigate the perception of biological motion at different processing levels.

## Methods

### Participants

Nineteen children and adolescents diagnosed with ASD and 17 TD matched controls participated. The eligibility criteria for ASD subjects were: (i) a clinical diagnosis of ASD based on best clinical judgment, the Autism Diagnostic Interview-Revised [Lord, Rutter, & Le Couteur, 1994], and the Autism Diagnostic Observation Schedule-Generic [Lord et al., 2000]; (ii) at least average intelligence (i.e., scoring  $\geq 75$ ) on the WAIS-R on the full scale, performance, and verbal IQ using the Wechsler Abbreviated Scale of Intelligence<sup>TM</sup> (WASI) [Wechsler, 1999]; (iii) no prior or concurrent diagnosis of any other neurological (e.g., epilepsy, Tourette's syndrome), psychiatric (e.g., childhood-onset schizophrenia), or developmental (e.g., ADHD) disorder; (iv) aged between 8 and 18 years. The eligibility criteria for TD controls were identical except for the diagnosis of ASD. The two groups were matched on age, gender and IQ as measured by the Wechsler Abbreviated Scale of Intelligence (Table 1). Three children in the ASD group were excluded because they gave the same action response on all trials (two participants), or trials in the different-location condition (one participant). Hence, the final sample for the ASD group included 16 children.

The TD group consisted of 13 males and 4 females, and the ASD group consisted of 12 males and 4 females. All children were right-handed. This study was approved by the UCLA Institutional Review Board for the Protection of Research Subjects, and written informed consent/assent was obtained from every subject.

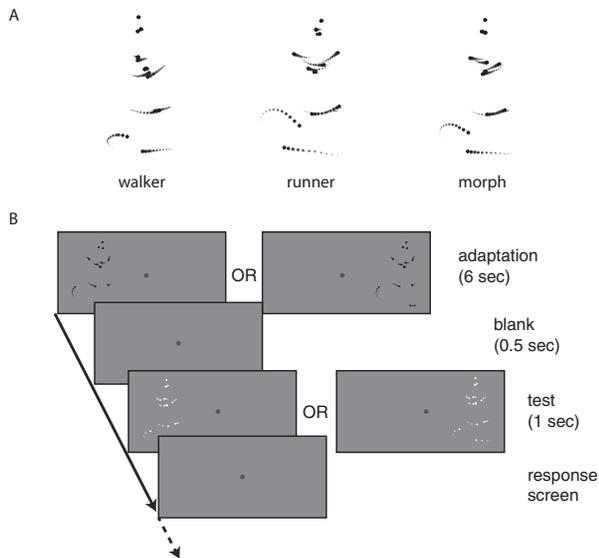
Based on a previous study [van Boxtel & Lu, 2013b], which used an identical paradigm but compared people with many vs. few autistic traits in the typical population, a power analysis (one-tailed *t*-test with power 0.8) revealed a required sample size of 17.

### Stimuli

In the adaptation experiment, stimuli were identical to those used in a previous study [van Boxtel & Lu, 2013b]. In brief, biological motion stimuli were viewed from a sagittal view, and displayed using the BiomotionToolbox [van Boxtel & Lu, 2013a]. Prototypical walking and running actions were generated from the Carnegie Mellon University (CMU) motion-capture database (<http://mocap.cs.cmu.edu>) and displayed as point-light stimuli [Johansson, 1973]. Horizontal whole-body movements were removed to display the action at a stationary location on the screen. All actions were facing rightward. The gait-cycle length was equated between walking and running actions (1 sec) to prevent participants from using this cue to recognize actions. The actions started at a random posture in the movement cycle.

This study used a morph action for a recognition task. The morph action was generated by linearly combining the joint trajectories of the two prototypical actions (walking and running) using a spatiotemporal morphing model developed by Giese and Poggio [2000]. A morph parameter controlled the similarity of the morph action to the prototypical actions. A morph parameter of 0 indicates a stereotypical running action, a value of 0.5 generates an ambiguous action between running and walking, and a value of 1 yields a stereotypical walking action. Figure 1A illustrates the joints' movement trajectories for a walker, runner, and morph action with a morphing parameter of 0.5.

The experiment was run on a laptop, positioned at a comfortable viewing distance from the participant. Although this distance was variable, the typical distance was between 45 and 50 cm. Actions were about 4.4°, and dot size was about 0.34°. The actions were displayed in the periphery, about 4.4° left or right from



**Figure 1.** Illustration of stimuli and paradigm used in adaptation blocks. (A) Joint trajectories for walking, running and morph action. For illustrational purposes, action frames are displayed with an increasingly dark color and an increasing size. During the actual stimulation only 13 dots were shown (one for each joint plus the head) in each frame. (B) The experimental procedure in the adaptation block. An adapting stimulus (either a prototypical walker or runner) was presented for 6 sec, on the left or right of fixation. After a brief blank, a 1-sec test stimulus of the morphed action was presented, either on the left or right of fixation.

fixation. The experiment was run in a room that was devoid of distractions.

#### Procedure

A discrimination block was first conducted to assess how participants discriminate between two actions. On each trial of the discrimination block, morphed actions were presented for 1 sec in the center of the display. Participants indicated whether they perceived the morphed action as walking or running. We used a 60-trial adaptive staircase [Prins & Kingdom, 2009] to estimate the morphing threshold at which the resulting morph action was perceived to be walking 50% of the time, and running 50% of the time (i.e., the point of subjective equality). We fitted a cumulative Gaussian function with the psi-marginal method to estimate the morphing threshold, which was used to generate test morph actions in the subsequent adaptation block. This threshold measurement had two objectives. First, it allowed us to determine whether there were differences in categorizing ambiguous actions between children with ASD and TD controls, possibly reflecting altered perceptual boundary between two action categories in ASD. Second, given the considerable phenotypic heterogeneity observed in ASD, obtaining individual morph-

ing values ensured that ambiguity in the test stimuli to be used in the subsequent adaptation block was equated across participants, as well as matched between the ASD and TD groups.

The second block presented the adaptation paradigm as shown in Figure 1B. Each trial started with a 6-sec adaptation period, followed by a 1-sec test stimulus of a morphed action after a 500-ms blank screen with a fixation cross. Adapting stimuli were a prototypical walking or running action, displayed with black point-lights either left or right of fixation. The test stimulus, a morphed action, was displayed with white point-lights on either sides of fixation, resulting in the same or different display location relative to the adapting stimuli. In each trial, participants indicated the type of action (walking or running) they perceived for the test stimuli.

Participants were asked to fixate the center cross. Prior studies in children with and without ASD in the same age range indicate no between-group differences in the ability to fixate on a center cross fixation tasks such as ours [Davies, Dapretto, Sigman, Sepeta, & Bookheimer, 2011; Greene et al., 2011; Sepeta et al., 2012]; nonetheless, the experimenter monitored fixation throughout the experiment, providing reminders as deemed necessary.

#### Dependent Measures: Local and Global Adaptation Strength

To quantify the strength of adaptation in the second block, we measured the proportion of trials that were reported as “runner” in each condition. An action adaptation effect would be revealed if more runner responses were obtained after adaptation to a walker than to a runner. Hence, we calculated the conditional proportion of runner responses depending on whether the adapting action was a walker or a runner. The difference between these two conditional proportions was defined as *adaptation strength*. Positive values of strength indicate an adaptation aftereffect. A difference of zero indicates the absence of an aftereffect, and negative values indicate a priming effect.

When the adapting and test locations were different, only location-invariant action adaptation was probed, presumably only reflecting high-level and global action adaptation [see van Boxtel & Lu, 2013b]. Hence, the global adaptation strength was defined as the difference between the two conditional proportions when the adapting and test locations were different. However, when the adapting and test locations were the same, adaptation at both the global level of action processing and the local level of location-specific motion processing was probed. Hence, the adaptation strength in the same-location condition reflects the combined influence of global and local adaptation. The local adaptation strength was, therefore, defined as the difference of

the adaptation strength in the same-location condition minus the adaptation strength measured in the different-location condition.

## Results

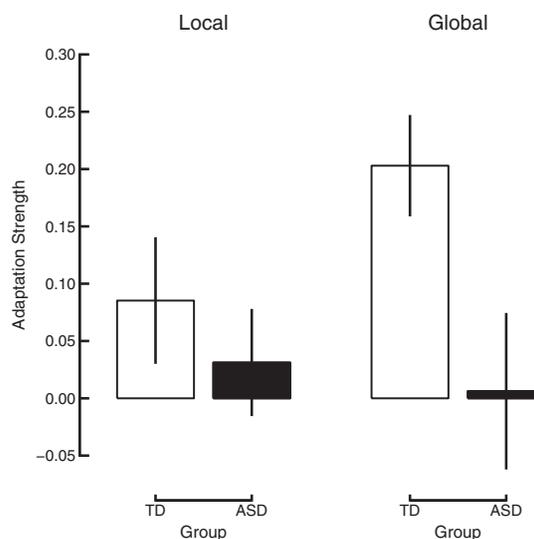
### *Intact Action Recognition in ASD*

The points of subjective equality (i.e., the perceptual boundary between walking and running categories) were  $0.42 \pm 0.05$  (mean  $\pm$  s.e.m.) for the ASD group and  $0.37 \pm 0.04$  for the TD group, which were not significantly different from each other ( $t(31) = 0.88$ ,  $P = 0.39$ , Cohen's  $d = 0.30$ ). Even after adjusting for full-scale IQ and age, an analysis of covariance (ANCOVA) revealed no group difference in perceptual boundaries between ASD and TD (all  $P > 0.4$ ), suggesting intact ability in ASD to recognize actions. This finding is consistent with a recent study by Cusack et al. [2015], showing that the perceptual system in people with ASD processes action information adequately, and form intact perceptual representations of other people's actions for detection and recognition.

### *Attenuated Adaptation to Actions in ASD*

Figure 2 depicts the strength of global and local adaptation for the ASD and TD groups. Planned comparisons showed that the TD group displayed no significant local adaptation ( $t(16) = 1.55$ ,  $P = 0.14$ , Cohen's  $d = 0.37$ ), but a strong global adaptation ( $t(16) = 4.59$ ,  $P = 0.0003$ , Cohen's  $d = 1.11$ ). This pattern was similar to that observed previously for college students with few autistic traits [van Boxtel & Lu, 2013b]. In contrast, the ASD group showed little adaptation at either processing level. Neither local ( $t(15) = 0.67$ ,  $P = 0.51$ ) nor global ( $t(15) = 0.09$ ,  $P = 0.93$ ) adaptation strengths were significant.

We performed a mixed-design ANCOVA, with group (TD, ASD) as a between-subject factor, adaptation level (global, local) as a within-subject factor, and age and full-scale IQ as covariates. We found a significant main effect of group ( $F(1,29) = 7.10$ ,  $P = 0.012$ ,  $\eta_p^2 = 0.197$ ), consistent with our analysis with planned comparisons indicating children with ASD showed weaker adaptation than the TD group. The two-way interaction between group and adaptation level was not significant ( $F(1,29) = 2.75$ ,  $P = 0.108$ ). We further examined the simple main effect to assess group differences for global adaptation and local adaptation separately. The TD group showed significantly greater global adaptation than the ASD group ( $F(1,29) = 4.43$ ,  $P = 0.044$ ,  $\eta_p^2 = 0.132$ , controlling for age and IQ). For local adaptation, we did not find a significant group difference between the two groups ( $F(1,29) = 0.78$ ,  $P = 0.39$ ,  $\eta_p^2 = 0.03$ ), suggesting that neither TD nor ASD children showed



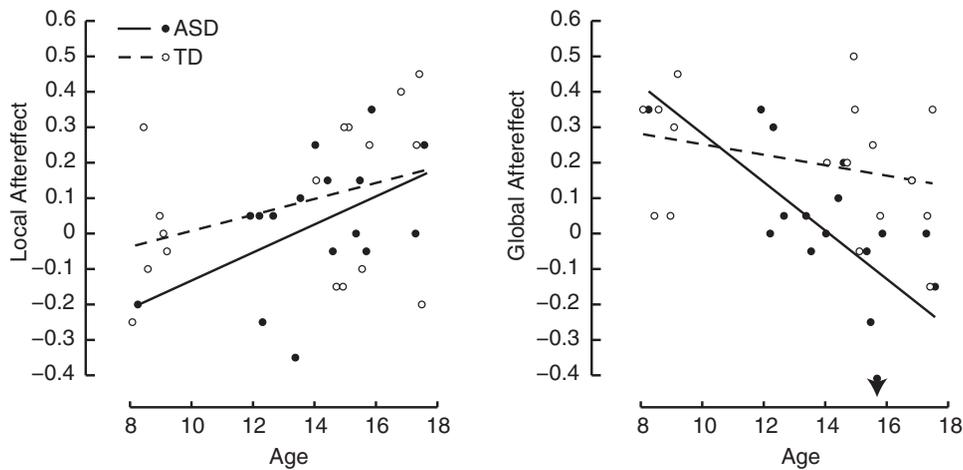
**Figure 2.** Adaptation strength for local and global adaptation in TD and ASD groups (means  $\pm$  s.e.m.). Local adaptation strength reflects adaptability at the low level of motion processing; global adaptation strength reflects adaptability at the high level of action processing.

strong adaptation at the local level of motion processing when viewing action stimuli.

We found a significant interaction between adaptation level and age ( $F(1,29) = 7.81$ ,  $P = 0.009$ ,  $\eta_p^2 = 0.212$ ), suggesting that the age-related changes in adaptation strength vary across different processing levels. The relation between age and adaptation strength is examined in more detail in next section.

### *Significant Correlation of Local and Global Adaptation Strength with Age in ASD*

Given the well-documented heterogeneity in the ASD population, we conducted multiple linear regression analyses on the ASD group to further examine the relationship between adaptation strength and the ADOS severity score, as well as full-scale IQ and age. For local motion adaptation, the three predictor variables accounted for 41.2% of the variability in the measured local adaptation strength. Local motion adaptation strength positively correlated with age (*simple correlation* = .49;  $P = .053$ ; *partial correlation* = .61,  $P = 0.02$  controlling for ADOS severity score and IQ), as shown in Figure 3. Even excluding the youngest child, the correlation of local motion adaptation with age remained relatively high (*partial correlation* = .55,  $P = 0.054$ ). Thus, older ASD children showed greater adaptation at the local motion processing level. Local adaptation strength did not correlate with ADOS severity score (*partial correlation* =  $-.47$ ,  $P = 0.09$ ), nor with IQ (*partial correlation* = .25,  $P = 0.39$ ).



**Figure 3.** Local and global adaptation strength correlate with age for the ASD group, but not for the TD group. Data for ASD participants are displayed with black filled circles, TD participants are displayed with white filled circles. Both local and global adaptation strengths were correlated with age in the ASD group. This correlation was positive for local adaptation but negative for global adaptation, in the ASD group. No significant correlations were found for the TD children. The plotted range on the y-axis was restricted from  $-0.4$  to  $0.6$ , to display the dependence on age, and have the same range for local and global affects. Data from one ASD child in the global adaptation plot fell outside this range (indicated by an arrow). The actual level was  $-0.8$ ; including or excluding this subject did not alter the statistical significance of the results.

For global action adaptation in children with ASD, multiple linear regression analyses revealed that the three predictor variables (i.e., ADOS severity score, full-scale IQ and age) accounted for 46.8% variability in the measured adaptation strength. Global adaptation strength was negatively correlated with the age in children with ASD (*simple correlation* =  $-.58$ ,  $P = .019$ ; *partial correlation* =  $-.56$ ,  $P = 0.036$ , controlling for ADOS score and IQ), suggesting that older ASD children adapt less at the global action processing level. Global adaptation strength did not correlate with ADOS score (*partial correlation* =  $-.28$ ,  $P = 0.33$ ), nor with IQ (*partial correlation* =  $.43$ ,  $P = 0.13$ ). The influence of age remained significant after excluding two possible outliers (a child aged 8 years, and a participant with a very negative global adaptation measure; *partial correlation* =  $-.58$ ,  $P = 0.049$ ).

Similar regression analysis for the TD group (without ADOS severity score as predictor), did not yield significant relationships between adaptation effects and either age or IQ score. None of the results changed in a qualitative way when full-scale IQ was replaced by performance IQ and verbal IQ, and neither measure of IQ reached significance as a predictor.

We also compared the ASD and TD group in terms of the impact of age on adaptation strength. The regression analysis included an interaction term of age  $\times$  group (ASD/TD), in addition to the other regressors of group, age, and full-scale IQ. We found a significant between-group difference in regression coefficient with age for the global adaptation measure ( $t(28) = 2.26$ ,  $P = 0.032$ ), but not for the local adaptation measure ( $P = 0.61$ ), confirming the above results that the impact

of age on action-level adaptation is significantly different in children with ASD than in TD children.

## Discussions

In this study, we measured how observers categorize and adapt to different biological motion stimuli. Compared to TD controls, youth with ASD had similar perceptual boundaries between the two action categories (i.e., walking vs. running), indicating intact ability in recognizing these actions.

In terms of adaptation, the TD group showed strong adaptation at the global level of action processing, and nearly absent adaptation at the local level of motion processing, consistent with previous findings for a typical population of college students with few autistic traits [van Boxtel & Lu, 2013b]. The ASD group did not show significant adaptation, either at the local or global processing level, suggesting that children with ASD have a weakened ability to adapt to recently observed actions. These results imply a decreased sensitivity to temporal context in ASD, which is consistent with the hypothesis of general impairment in global processing in ASD [Happé & Frith, 2006; Mottron, Dawson, Soulières, Hubert, & Burack, 2006].

Interestingly, research on face perception has yielded a similar pattern of results on recognition and adaptation. While there is no unequivocal support for difficulties in face detection and identification in ASD [Simmons et al., 2009; Weigelt, Koldewyn, & Kanwisher, 2012], several studies have reported significant impairments in face

adaptation for youth with ASD [Ewing, Leach, Pellicano, Jeffery, & Rhodes, 2013a; Pellicano, Jeffery, Burr, & Rhodes, 2007], although not in adults [Cook, Brewer, Shah, & Bird, 2014].

Why do youth with ASD show typical perceptual boundaries between action categories in a discrimination task, but attenuated adaptation for faces and biological motion stimuli? Though speculative, the difference between discriminability and adaptability in ASD may reflect the fact that the two tasks involve low-level and high-level processing to different degrees. To discriminate a walker from a runner, one could adequately make discriminations based on some local critical features, such as the movements of feet and lower arms for a briefly presented action stimulus, leading to similar discrimination behavior for ASD and TD groups. However, any reduction in activation of the action processing system may lead to a grossly diminished accumulated activity over time. Because adaptation reflects this accumulated activity (being inversely proportional to it), small deficiencies that do not influence discrimination could accumulate over time, and may be revealed only when adaptation strength is measured. This hypothesis may explain why some studies have found differences in brain activity between ASD and TD participants even when no behavioral deficits were observed for ASD participants in biological motion discrimination [Freitag et al., 2008; Herrington et al., 2007; Kaiser et al., 2010b; McKay et al., 2012] or facial emotional expressions [Dapretto et al., 2006].

#### *The Impact of Age on Adaptation to Biological Motion*

Even though we found no overall average adaptation effects at local and global levels in ASD, our analyses did reveal a relation between age and adaptation at different processing levels within the ASD group. We found that global action processing in children with ASD adapts less with increased age, whereas local motion processing adapts more with age. Such relations between age and adaptation at different processing levels were not found in the TD group.

These age-related changes in biological motion adaptation may appear inconsistent with a recent meta-analysis that concluded that there were no clear age-related effects in global and local processing [Van der Hallen et al., 2015]; however, that study explicitly excluded dynamic stimuli. Other studies that did examine biological motion have suggested that age may have an important influence on biological motion processing in ASD [Kaiser & Pelphrey, 2012; Murphy et al., 2009], whereas others did not [Annaz et al., 2010; Cusack et al., 2015; McKay et al., 2012]. Specifically, previous studies have shown evidence that global processing [Scherf, Luna, Kimchi, Minshew, & Behrmann,

2008] and specifically biological motion processing [Annaz et al., 2010] may improve with age in TD individuals, but not in ASD.

In this study, we specifically examined children in late childhood and adolescence. The transition from late childhood to adolescence is an important developmental period because many behavioral and cognitive changes take place at this time [Blakemore & Choudhury, 2006]. At the same time, this is also an important period for brain development, specifically in relation to social cognition [e.g., Blakemore & Mills, 2014; Giedd et al., 2009; Pelphrey & Carter, 2008; Vander Wyk, Voos, & Pelphrey, 2012], with developmental changes also reported in the superior temporal sulcus [Vander Wyk et al., 2012], a region implicated in the processing of biological motion. Thus, significant changes in biological motion processing can be expected to occur in this age range, including changes in local and global processing, as suggested by our findings. Although we did not use a longitudinal design, the weakened processing at a global level in our ASD sample is not suggestive of a delayed developmental trajectory, as older children with ASD showed weaker adaptation to actions than younger children with ASD.

We tentatively suggest two reasons for the different associations with age observed for local and global adaptation in children with and without ASD. First, these differences may result from the development of a compensatory mechanism in the ASD group, based on increasingly recruiting robust local processing, whereas global processing remains underdeveloped. Alternatively, older individuals may have an increased preference for local processing at the expense of global processing. Either hypothesis is consistent with our findings. Furthermore, these proposed hypotheses could potentially explain why recognition tasks show no clear deficit in ASD, as these tasks can be performed based on either local or global cues, or both. Only a task designed to specifically gauge global processing, such as the present global adaptation task, is likely to reveal a deficit.

#### *No Dependence on IQ and Severity Scores*

Previous studies have reported that for biological motion tasks, IQ is an important factor affecting perception in individuals with ASD [Jones et al., 2011; Koldewyn et al., 2010; Rutherford & Troje, 2012]. For example, Koldewyn et al. [2010] reported reduced coherent motion discrimination and biological motion discrimination in ASD relative to TD controls, but after controlling for IQ, only performance in a biological motion task showed a significant group difference. Others have suggested that only a subset of ASD individuals—those with low IQ—show deficits in biological

motion processing [Jones et al., 2011]. In this study, we found that IQ did not play a significant role in any of our tasks, regardless of whether we used full-scale IQ, or verbal and performance IQ as predictor variables. However, our sample was restricted to participants with an IQ of at least 75; hence, we may have missed the subset of low-IQ individuals who would show poor biological motion perception.

Other studies have reported a relationship between task performance and severity of autism symptomatology. For example, Blake et al. [2003] showed that recognition performance for biological motion stimuli was impaired in their ASD sample, but more heavily so in those individuals with higher ADOS [Lord et al., 2000] severity scores, or higher scores on the Childhood Autism Rating Scale [Schopler, Reichler, DeVellis, & Daly, 1980]. Similarly, Pellicano et al. [2007] showed that face adaptation was more severely impaired in individuals with higher scores on the Social Communication Questionnaire [SCQ; Rutter, Bailey, & Lord, 2003]. We did not observe a significant relation between adaptation strengths and ADOS severity score in our task. However, it should be mentioned that the multiple regression analysis did find a trending result (partial correlation =  $-.47$ ,  $P = 0.09$ ) whereby local adaptation strength tended to decrease with higher ADOS severity scores. It is, therefore, possible that a larger sample size might reveal a relationship between adaptation to biological motion and ADOS severity scores.

#### *Possible Mechanisms Underlying Attenuated Adaptation in Autism*

We did not study nonbiological motion stimuli, and, therefore, cannot ascertain that the observed adaptation effects in ASD are specific to biological motion. However, current evidence suggests a deficit specific to the processing of social stimuli, with children with ASD showing decreased adaptation to both biological motion (this study) and face stimuli [Ewing, Pellicano, & Rhodes, 2013b; Pellicano et al., 2007], but no difference in either detection [Kaiser, Delmolino, Tanaka, & Shiffrar, 2010a] or adaptation [Ewing et al., 2013b; Karaminis et al., 2015] to non-social stimuli.

Also, two distinct mechanisms may underlie our findings. The reduced global aftereffect in ASD may reflect decreased adaptability per se. Alternatively, it may reflect decreased attention to social (i.e., faces and biological motion) stimuli [e.g., Annaz, Campbell, Coleman, Milne, & Swettenham, 2012; van Boxtel & Lu, 2013b]. Future experiments with tighter experimental control over attention allocation are needed to differentiate between these two possibilities.

A weakened adaptability in ASD for face and biological motion stimuli is consistent with findings indicating that individuals with ASD are impaired in contextual

processing [Bölte, Holtmann, Poustka, Scheurich, & Schmidt, 2007; Brosnan, Scott, Fox, & Pye, 2004; Happé, 1997; Jolliffe & Baron-Cohen, 2001]. Such findings suggest that people with ASD may be more likely to perceive objects the way they are [Pellicano & Burr, 2012], and be less sensitive to illusions. This view would also predict that adaptation (as a type of temporal contextual processing) would be decreased in ASD, independent of whether the type of adaptation is local or global, or the adapted stimulus is socially relevant or not. However, an alternative hypothesis from a hierarchical perspective predicts that reduced global processing will be accompanied by increased local processing [van Boxtel & Lu, 2013c; Van de Cruys et al., 2014].

The present results provide support for both hypotheses. When average adaptation level was examined for the ASD group, neither local nor global processing scores were significantly above zero, suggesting a general tendency to ignore contextual prior information in ASD. When heterogeneity within the ASD group was examined, we found increases in local processing and decreases in global processing with age, supporting the hierarchical hypothesis based on predictive coding. To further illuminate the mechanisms by which visual adaptation is altered in ASD, additional work is needed to examine how ASD affects adaptation to different sensory stimuli.

#### **Acknowledgments**

The authors thank Devi Beck-Pancer and Rosemary McCarron for their help with data collection, and the reviewers for their valuable comments. This research was supported by the UCLA Center for Autism Research and Training (CART) pilot grant and NSF grant BCS-0843880 to HL, and grant NICHD P50 HD055784 from the Eunice Kennedy Shriver National Institute of Child Health and Human Development to MD.

#### **References**

- Annaz, D., Campbell, R., Coleman, M., Milne, E., & Swettenham, J. (2012). Young children with autism spectrum disorder do not preferentially attend to biological motion. *Journal of Autism and Developmental Disorders*, 42(3), 401–408.
- Annaz, D., Remington, A., Milne, E., Coleman, M., Campbell, R., Thomas, M.S., et al. (2010). Development of motion processing in children with autism. *Developmental Science*, 13(6), 826–838.
- Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2003). Motion perception in autism: A “complex” issue. *Journal of Cognitive Neuroscience*, 15(2), 218–225.
- Blake, R., Turner, L.M., Smoski, M.J., Pozdol, S.L., & Stone, W.L. (2003). Visual recognition of biological motion is impaired in children with autism. *Psychological Science*, 14(2), 151–157.

- Blakemore, S.J., & Choudhury, S. (2006). Development of the adolescent brain: Implications for executive function and social cognition. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, 47(3–4), 296–312.
- Blakemore, S.J., & Mills, K.L. (2014). Is adolescence a sensitive period for sociocultural processing? *Annual Review of Psychology*, 65, 187–207.
- Bölte, S., Holtmann, M., Poustka, F., Scheurich, A., & Schmidt, L. (2007). Gestalt perception and local-global processing in high-functioning autism. *Journal of Autism and Developmental Disorders*, 37(8), 1493–1504.
- Brosnan, M.J., Scott, F.J., Fox, S., & Pye, J. (2004). Gestalt processing in autism: Failure to process perceptual relationships and the implications for contextual understanding. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, 45(3), 459–469.
- Casile, A., & Giese, M.A. (2005). Critical features for the recognition of biological motion. *Journal of Vision*, 5(4), 348–360.
- Cook, R., Brewer, R., Shah, P., & Bird, G. (2014). Intact facial adaptation in autistic adults. *Autism Research*, 7(4), 481–490.
- Cusack, J.P., Williams, J.H., & Neri, P. (2015). Action perception is intact in autism spectrum disorder. *Journal of Neuroscience*, 35(5), 1849–1857.
- Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron*, 48(3), 497–507.
- Dapretto, M., Davies, M.S., Pfeifer, J.H., Scott, A.A., Sigman, M., Bookheimer, S.Y., et al. (2006). Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience*, 9(1), 28–30.
- Davies, M.S., Dapretto, M., Sigman, M., Sepeta, L., & Bookheimer, S.Y. (2011). Neural bases of gaze and emotion processing in children with autism spectrum disorders. *Brain and Behaviour*, 1(1), 1–11.
- de la Rosa, S., Streuber, S., Giese, M., Bulthoff, H.H., & Curio, C. (2014). Putting actions in context: Visual action adaptation aftereffects are modulated by social contexts. *PLoS One*, 9(1), e86502.
- Ewing, L., Leach, K., Pellicano, E., Jeffery, L., & Rhodes, G. (2013a). Reduced face aftereffects in autism are not due to poor attention. *PLoS One*, 8(11), e81353.
- Ewing, L., Pellicano, E., & Rhodes, G. (2013b). Atypical updating of face representations with experience in children with autism. *Developmental Science*, 16(1), 116–123.
- Freitag, C.M., Konrad, C., Haberlen, M., Kleser, C., von Gontard, A., Reith, W., et al. (2008). Perception of biological motion in autism spectrum disorders. *Neuropsychologia*, 46(5), 1480–1494.
- Frisby, J.P. (1979). *Seeing: Illusion, brain and mind*. Oxford: Oxford University Press.
- Frith, U. (1989). *Autism: Explaining the enigma*. Oxford: Blackwell.
- Giedd, J.N., Lalonde, F.M., Celano, M.J., White, S.L., Wallace, G.L., Lee, N.R., et al. (2009). Anatomical brain magnetic resonance imaging of typically developing children and adolescents. *Journal of the American Academy of Child and Adolescent Psychiatry*, 48(5), 465–470.
- Giese, M.A., & Poggio, T. (2000). Morphable models for the analysis and synthesis of complex motion patterns. *International Journal of Computer Vision*, 38(1), 59–73.
- Greene, D.J., Colich, N., Iacoboni, M., Zaidel, E., Bookheimer, S.Y., & Dapretto, M. (2011). Atypical neural networks for social orienting in autism spectrum disorders. *Neuroimage*, 56(1), 354–362.
- Grossman, E.D., Jardine, N.L., & Pyles, J.A. (2010). fMR-adaptation Reveals invariant coding of biological motion on the human STS. *Frontiers in Human Neuroscience*, 4, 15.
- Happé, F. (1997). Central coherence and theory of mind in autism: Reading homographs in context. *British Journal of Developmental Psychology*, 15(1), 1–12.
- Happé, F., & Frith, U. (2006). The weak coherence account: Detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 36(1), 5–25.
- Herrington, J.D., Baron-Cohen, S., Wheelwright, S.J., Singh, K.D., Bullmore, E.T., Brammer, M., et al. (2007). The role of MT+/V5 during biological motion perception in Asperger syndrome: An fMRI study. *Research in Autism Spectrum Disorders*, 1(1), 14–27.
- Hubert, B., Wicker, B., Moore, D.G., Monfardini, E., Duverger, H., Da Fonseca, D., et al. (2007). Brief report: recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *Journal of Autism and Developmental Disorders*, 37(7), 1386–1392.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics*, 14(2), 201–211.
- Jolliffe, T., & Baron-Cohen, S. (2001). A test of central coherence theory: can adults with high-functioning autism or Asperger syndrome integrate fragments of an object? *Cognitive Neuropsychiatry*, 6(3), 193–216.
- Jones, C.R., Swettenham, J., Charman, T., Marsden, A.J., Tregay, J., Baird, G., et al. (2011). No evidence for a fundamental visual motion processing deficit in adolescents with autism spectrum disorders. *Autism Research*, 4(5), 347–357.
- Kaiser, M.D., Delmolino, L., Tanaka, J.W., & Shiffrar, M. (2010a). Comparison of visual sensitivity to human and object motion in autism spectrum disorder. *Autism Research*, 3(4), 191–195.
- Kaiser, M.D., Hudac, C.M., Shultz, S., Lee, S.M., Cheung, C., Berken, A.M., et al. (2010b). Neural signatures of autism. *Proceedings of the National Academy of Sciences of the United States of America*, 107(49), 21223–21228.
- Kaiser, M.D., & Pelphrey, K.A. (2012). Disrupted action perception in autism: Behavioral evidence, neuroendophenotypes, and diagnostic utility. *Developmental Cognitive Neuroscience*, 2(1), 25–35.
- Kaiser, M.D., & Shiffrar, M. (2009). The visual perception of motion by observers with autism spectrum disorders: A review and synthesis. *Psychonomic Bulletin and Review*, 16(5), 761–777.
- Karaminis, T., Turi, M., Neil, L., Badcock, N.A., Burr, D., & Pellicano, E. (2015). Atypicalities in perceptual adaptation in autism do not extend to perceptual causality. *PLoS One*, 10(3), e0120439.
- Klin, A., Lin, D.J., Gorrindo, P., Ramsay, G., & Jones, W. (2009). Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature*, 459(7244), 257–261.

- Knapen, T., Rolfs, M., & Cavanagh, P. (2009). The reference frame of the motion aftereffect is retinotopic. *Journal of Vision*, 9(5), 16 11–17.
- Kohn, A., & Movshon, J.A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience*, 7(7), 764–772.
- Koldewyn, K., Jiang, Y.V., Weigelt, S., & Kanwisher, N. (2013). Global/local processing in autism: Not a disability, but a disinclination. *Journal of Autism and Developmental Disorders*, 43(10), 2329–2340.
- Koldewyn, K., Whitney, D., & Rivera, S.M. (2010). The psychophysics of visual motion and global form processing in autism. *Brain*, 133(Pt 2), 599–610.
- Kovacs, G., Cziraki, C., Vidnyanszky, Z., Schweinberger, S.R., & Greenlee, M.W. (2008). Position-specific and position-invariant face aftereffects reflect the adaptation of different cortical areas. *Neuroimage*, 43(1), 156–164.
- Lange, J., & Lappe, M. (2006). A model of biological motion perception from configural form cues. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, 26(11), 2894–2906.
- Lee, A.L., & Lu, H. (2012). Two forms of aftereffects induced by transparent motion reveal multilevel adaptation. *Journal of Vision*, 12(4), 1–13.
- Lord, C., Risi, S., Lambrecht, L., Cook, E.H. Jr., Leventhal, B.L., DiLavore, P.C., et al. (2000). The autism diagnostic observation schedule-generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, 30(3), 205–223.
- Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism diagnostic interview-revised: A revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders*, 24(5), 659–685.
- Lu, H. (2010). Structural processing in biological motion perception. *Journal of Vision*, 10(12), 13, 1–13.
- McKay, L.S., Simmons, D.R., McAleer, P., Marjoram, D., Piggot, J., & Pollick, F.E. (2012). Do distinct atypical cortical networks process biological motion information in adults with autism spectrum disorders? *Neuroimage*, 59(2), 1524–1533.
- Milne, E., & Szczerbinski, M. (2009). Global and local perceptual style, field-independence, and central coherence: An attempt at concept validation. *Advances in Cognitive Psychology*, 5, 1–26.
- Moore, D.G., Hobson, R.P., & Lee, A. (1997). Components of person perception: An investigation with autistic, non-autistic retarded and typically developing children and adolescents. *British Journal of Developmental Psychology*, 15, 401–423.
- Mottron, L., Dawson, M., Soulières, I., Hubert, B., & Burack, J. (2006). Enhanced perceptual functioning in autism: An update, and eight principles of autistic perception. *Journal of Autism and Developmental Disorders*, 36(1), 27–43.
- Murphy, P., Brady, N., Fitzgerald, M., & Troje, N.F. (2009). No evidence for impaired perception of biological motion in adults with autistic spectrum disorders. *Neuropsychologia*, 47(14), 3225–3235.
- Nackaerts, E., Wagemans, J., Helsen, W., Swinnen, S.P., Wenderoth, N., & Alaerts, K. (2012). Recognizing biological motion and emotions from point-light displays in autism spectrum disorders. *PLoS One*, 7(9), e44473.
- Parron, C., Da Fonseca, D., Santos, A., Moore, D.G., Monfardini, E., & Deruelle, C. (2008). Recognition of biological motion in children with autistic spectrum disorders. *Autism: the international journal of research and practice*, 12(3), 261–274.
- Pavlova, M.A. (2012). Biological motion processing as a hallmark of social cognition. *Cerebral Cortex*, 22(5), 981–995.
- Pellicano, E., & Burr, D. (2012). When the world becomes ‘too real’: A Bayesian explanation of autistic perception. *Trends in Cognitive Sciences*, 16(10), 504–510.
- Pellicano, E., Jeffery, L., Burr, D., & Rhodes, G. (2007). Abnormal adaptive face-coding mechanisms in children with autism spectrum disorder. *Current Biology: CB*, 17(17), 1508–1512.
- Pelphrey, K.A., & Carter, E.J. (2008). Brain mechanisms for social perception: Lessons from autism and typical development. *Annals of the New York Academy of Sciences*, 1145, 283–299.
- Prins, N., & Kingdom, F. (2009). Palamedes: Matlab routines for analyzing psychophysical data. Available at: <http://www.palamedestoolbox.org>. Accessed 11 January 2016.
- Rutherford, M.D., & Troje, N.F. (2012). IQ predicts biological motion perception in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 42(4), 557–565.
- Rutter, M., Bailey, A., & Lord, C. (2003). *SCQ: Social communication questionnaire*. Los Angeles, CA: Western Psychological Services.
- Saygin, A.P., Cook, J., & Blakemore, S.J. (2010). Unaffected perceptual thresholds for biological and non-biological form-from-motion perception in autism spectrum conditions. *PLoS One*, 5(10), e13491.
- Scherf, K.S., Luna, B., Kimchi, R., Minshew, N., & Behrmann, M. (2008). Missing the big picture: Impaired development of global shape processing in autism. *Autism Research*, 1(2), 114–129.
- Schopler, E., Reichler, R.J., DeVellis, R.F., & Daly, K. (1980). Toward objective classification of childhood autism: Childhood autism rating scale (CARS). *Journal of Autism and Developmental Disorders*, 10(1), 91–103.
- Segeta, L., Tsuchiya, N., Davies, M.S., Sigman, M., Bookheimer, S.Y., & Dapretto, M. (2012). Abnormal social reward processing in autism as indexed by pupillary responses to happy faces. *Journal of Neurodevelopmental Disorders*, 4(1), 17, 1–9.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States of America*, 105(2), 809–813.
- Simmons, D.R., Robertson, A.E., McKay, L.S., Toal, E., McAleer, P., & Pollick, F.E. (2009). Vision in autism spectrum disorders. *Vision Research*, 49(22), 2705–2739.
- Thurman, S.M., & Lu, H. (2013). Physical and biological constraints govern perceived animacy of scrambled human forms. *Psychological Science*, 24(7), 1133–1141.
- Troje, N.F., Sadr, J., Geyer, H., & Nakayama, K. (2006). Adaptation aftereffects in the perception of gender from biological motion. *Journal of Vision*, 6(8), 850–857.

- Troje, N.F., & Westhoff, C. (2006). The inversion effect in biological motion perception: Evidence for a “life detector”? *Current Biology*, 16(8), 821–824.
- van Boxtel, J.J.A., Alais, D., & van Ee, R. (2008). Retinotopic and non-retinotopic stimulus encoding in binocular rivalry and the involvement of feedback. *Journal of Vision*, 8(5):17, 1–10.
- van Boxtel, J.J.A., & Lu, H. (2012). Signature movements lead to efficient search for threatening actions. *PLoS One*, 7(5), e37085.
- van Boxtel, J.J.A., & Lu, H. (2013a). A biological motion toolbox for reading, displaying, and manipulating motion capture data in research settings. *Journal of Vision*, 13(12), 1–16.
- van Boxtel, J.J.A., & Lu, H. (2013b). Impaired global, and compensatory local, biological motion processing in people with high levels of autistic traits. *Frontiers in Psychology*, 4:209(209), 1–10.
- van Boxtel, J.J.A., & Lu, H. (2013c). A predictive coding perspective on autism spectrum disorders. *Frontiers in Psychology*, 4(19), 1–3.
- van Boxtel, J.J.A., & Lu, H. (2015). Joints and their relations as critical features in action discrimination: Evidence from a classification image method. *Journal of Vision*, 15(1), 1–17.
- Van de Cruys, S., Evers, K., Van der Hallen, R., Van Eylen, L., Boets, B., de-Wit, L., et al. (2014). Precise minds in uncertain worlds: predictive coding in autism. *Psychological Review*, 121(4), 649–675.
- Van der Hallen, R., Evers, K., Brewaeys, K., Van den Noortgate, W., & Wagemans, J. (2015). Global processing takes time: A meta-analysis on local-global visual processing in ASD. *Psychological Bulletin*, 141(3), 549–573.
- Vander Wyk, B.C., Voos, A., & Pelphrey, K.A. (2012). Action representation in the superior temporal sulcus in children and adults: An fMRI study. *Developmental Cognitive Neuroscience*, 2(4), 409–416.
- Wechsler, D. (1999). Wechsler abbreviated scale of intelligence. New York, NY: The Psychological Corporation: Harcourt Brace & Company.
- Weigelt, S., Koldewyn, K., & Kanwisher, N. (2012). Face identity recognition in autism spectrum disorders: A review of behavioral studies. *Neuroscience and Biobehavioral Reviews*, 36(3), 1060–1084.