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ABSTRACT
Autistic traits span a wide spectrum of behavioural departures from typical function. Despite the heterogeneous nature of autism spectrum disorder (ASD), there have been attempts at formulating unified theoretical accounts of the associated impairments in social cognition. A class of prominent theories capitalizes on the link between social interaction and visual perception: effective interaction with others often relies on discrimination of subtle non-verbal cues. It has been proposed that individuals with ASD may rely on poorer perceptual representations of other people's actions as returned by dysfunctional visual circuitry, and that in turn this may lead to less effective interpretation of those actions for social behaviour. It remains unclear whether such perceptual deficits exist in ASD: the evidence currently available is limited to specific aspects of action recognition, and the reported deficits are often attributable to cognitive factors that may not be strictly visual (e.g. attention). We present results from an exhaustive set of measurements spanning the entire action processing hierarchy, from motion detection to action interpretation, designed to factor out effects that are not selectively relevant to this function. Our results demonstrate that the ASD perceptual system returns functionally intact signals for interpreting other people's actions adequately; these signals can be accessed effectively when autistic individuals are prompted and motivated to do so under controlled conditions. However, they may fail to exploit them adequately during real-life social interactions.

INTRODUCTION

Autism spectrum disorder (ASD) is diagnosed exclusively on a behavioural basis, and is associated with impaired skills for social interaction (Lord et al. 2000). Current theoretical accounts hypothesize that it may derive from poor perceptual recognition or interpretation of other people's actions (Simmons et al., 2009). Previous experimental research on this question has focused on sensitivity to detection of biological motion (BM) within point light displays, but has yielded conflicting results (Atkinson 2009; Blake et al. 2003; Hubert et al. 2007; Jones et al. 2011; Koldewyn et al. 2010; Murphy et al. 2009; Nackaerts et al., 2013; Rutherford and Troje 2012; Saygin et al. 2010). There are several possible causes for these apparent inconsistencies in the literature.

First, inadequate experimental controls mean that group differences not specific to either ASD or the capacity for motion processing may generate effects. For example, impairments affecting any stage of visual processing prior to that concerned with the detection of biological motion may impact upon action processing (Neri et al, 2007). Similarly, some experimental tasks place high demands upon attention, working memory and decision-making capacity); these could feasibly be affected by impairments of executive function in ASD (Hill, 2004).

Second, a specific aspect of biological motion perception might only be disrupted in autism, making detection of group differences task-dependent. One hypothesis is that BM perception relies on a capacity for perception of the gestalt, so that while perception of whole figures is disrupted, detection of individual joint movement is intact (Happe and Frith 2006; Mottron et al. 2006; Simmons et al. 2009). Alternatively, knowledge of action could enhance perception via feedback, and this mechanism could be impaired in autism (Klin et al, 2003). A third hypothesis is that the temporal patterns of motion which lend moving objects a sense of animacy (e.g. the Heider and Simmel tasks, 1936, Viviani & Stucchi, 1992) are critical to BM perception, and processing of these patterns is impaired in autism (Castelli et al, 2000; Castelli et al, 2002; Rutherford et al, 2006).

In this study, comparing typically developing (TD) and ASD adolescents with normal Intelligence Quotient (IQ), we sought to rectify these limitations in two ways. First, we controlled for nonspecific effects by including an inversion condition (Neri et al. 2007; Pavlova and Sokolov 2000). A marked effect of inversion is one of the longest established features of BM perception from point-light displays (Sumi, 1984; Troje, 2006). Therefore, any deficit in BM perception will affect detection in an upright stimulus more than an inverted stimulus. Second, we carried out a comprehensive set of experimental manipulations spanning the action processing hierarchy, each experiment focussing on a specific cognitive function required for the detection of BM. This programme was deployed in a consistent, cross-checked manner, adopting a common set of tools, measurements and logic across the board. Overall, our behavioural results showed a non-significant trend towards impaired performance in ASD, but the performance between groups was remarkably similar after factoring out any aspecific effects with an inverted control condition.

METHODS

We settled on 6 experiments, each designed to test for a deficit of a specific aspect of action perception in autism. All experiments utilised point-light displays and a binary choice design. First, we probed the basic capacity to differentiate between biological motion and non-biological motion (Experiment 1, see below). Next, we sought to measure: the capacity to discriminate linear from animate motion of local joint movements (Experiment 2); the capacity to discriminate one form of action from another (Expriment 3); the two-stage hierarchical integration of local information (limbs) to full body agents (Experiment 4); the higher-level capacity to distinguish between two agents who are temporally synchronous from those who are not (Experiment 5); and generic attention to biological motion signals (Experiment 6).

Stimulus

Point-light action sequences depicted ~20 seconds of fighting or dancing at a sampling rate of 60 Hz; each sequence tracked 26 joint trajectories (13 per agent: head, shoulders, elbows, wrists, hips, knees, feet). Details of how these sequences were acquired are available from previous publications (Neri et al., 2006, 2007; Luu and Levi, 2013).

Participant Data

The research was ethically approved by the North of Scotland Research Ethics Committee. Participants were included if they had IQ>75 and no known visual impairment after correction with refractive lenses. Participants were adolescent males (ASD: mean age=16.09 years, SD=2.24; TD: mean age=15.54, SD=2.15; see also Figure 1B).

IQ was assessed with the Wechsler Abbreviated Scale of Intelligence (Wechsler 1999) and was in the normal range for all individuals (ASD: mean=103.14, SD=11.59; TD: mean=104.79, SD=9.14; see also Figure 1A for individual IQ results).

All ASD participants had an existing clinical diagnosis of ASDand were recruited at dedicated units within schools that specifically catered for ASD (Bolte et al. 2008). The existing diagnosis was verified by Autism Diagnostic Interview (Revised - Lord et al., 2000) with severity at time of testing indexed by total score on the Social Responsiveness Scale (SRS - Constantino and Gruber 2005). Scores showed no overlap between groups (ASD: mean =107.95, SD=26.56; TD: mean=13.79, SD=9.82; see also Figure 1).

We recruited 26 ASD participants and 22 TD participants in total. It was not practically feasible to recruit every participant for every task given the minimum amount of testing time required from each participant and the constraints associated with the maximum temporal window available for data collection in any given session. Instead, we sampled from the group we had available at the mutual convenience of researchers and participants. In experiments 1 and 5 there were 18 participants for each group. In the remaining experiments (2, 3, 4, 6), 15 participants from each group took part.

Experimental setup

Participants sat in front of a laptop with a 13.1 inch LCD screen (resolution 1024 x 840 pixels, refresh rate 60hz); viewing distance was loosely controlled between 80-120cm (no strict viewing distance was enforced but participants were instructed to remain seated in front of the display in upright posture, and were monitored continuously to verify they did so). We ensured that the experiment took place in an environment that was both suitable for undertaking visual psychophysical experiments (quiet, moderate lighting, no distraction), and comfortable/familiar for the participant (unfamiliar environments may affect performance in autistic populations).

General Methodology

We now describe protocol details that applied to most experiments, and later highlight relevant departures. Tasks structure conformed to the 2-alternative forced choice (2AFC) design or one-interval variants with symmetric binary choice (Green and Swets, 1966). Observers saw two intervals on each trial, presented in random order and separated by a 0.5-sec gap. The ‘target’ interval showed a 1.5-sec segment randomly selected from the original fighting sequence (see example in Figure 2A), while the ‘non-target' interval showed a scrambled version of another segment from the same sequence (see example in Figure 2C). Participants were asked to indicate the target interval by pressing one of two keys. Each experiment consisted of 2 sessions of 150 trials per participant.

Joint trajectories were sampled by 12 dots (size ~3 mm) with a limited lifetime of 150 ms (Neri et al., 1998); half the dots were bright (100% contrast) and half dark on a grey background (luminance ~30 cd/m^2). The fighting scene spanned ~20x13 cms (WxH). Size/luminance details are approximate because it was often necessary to test observers in variable environments where they felt most comfortable (see above).

Outcome variables

The primary outcome variable for the first 3 experiments was that of noise tolerance (Neri et al., 1998). Intervals of action sequences were masked by noise dots (each created by randomly sampling frames from a joint from the original action sequence and plotting it on a random location on the screen). The number of noise dots was varied in linear steps (Figure 3A-D) to derive full psychometric curves (Figure 3E-G). In the second set of experiments, designed to investigate reliance on global versus local features (Experiment 4) and sensitivity to interaction between agents (Experiment 5), we employed scrambling thresholds rather than noise dots (Neri et al., 2006). Joint trajectories in the ‘non-target’ sequence were randomly shifted in time either on a limb-by-limb basis (Figure 2E-F) or between agents (Figure 2G-H), and the amount of phase scrambling was varied. In the final experiment (6), designed to probe attention, the outcome variable was duration of contrast change.

Threshold estimation

Our goal was to extend our measurements to a wide class of stimuli and manipulations. The potential challenges associated with an experimental programme of this kind are illustrated by the psychometric curves in Figure 3E-G. In view of the large numbers of trials required and the consequently high demands placed upon participants, characterization of full psychometric curves has rarely been attempted before with ASD participants (Koldewyn et al. 2010). We found threshold measurements to be occasionally comparable to those obtained in TD participants (compare Figure 3E (TD)

with 3G), but more often ASD participants generated noisier data (example in Figure 3F) despite their IQ being within normal range (see Figure 1A). The parameters we finally adopted were the result of extensive piloting to maximize the robustness of our procedures. Thresholds were estimated by averaging the noise intensity values associated with a performance range between 60% and 90% percent of correct responses (Baldassi et al. 2006). This procedure allowed us to estimate thresholds from data that was too noisy to support robust fitting. Effects of conditions were tested for within groups using paired t-tests. Group differences were tested with an unpaired t-test comparing the log-ratio of upright/inverted thresholds across participants.

Individual experiments

Experiment 1: Upright vs inverted

Participants were asked to discriminate between a biological motion sequence (target) and a randomized motion sequence derived from the original sequence (non-target). The target sequence was a randomly selected 1.5 sec clip from the ~20 sec original sequence (Figure 2A-B). The non-target sequence (also 1.5 sec duration) was generated by selecting each joint randomly from a different time point in the original sequence, such that animate motion dynamics were maintained but coherence was lost (Figure 2C-D). There were two experimental conditions (mixed within blocks): upright and inverted. On inverted trials, both target and non-target stimuli were flipped upside-down.

Experiment 2: Animate vs Linear motion.

This experiment was almost identical to Experiment 1, except the inverted condition was replaced by a 'robotic' condition: the motion of each joint was undersampled and linearly interpolated, thus removing the animate characteristic of motion trajectories seen in biological motion. Consequently, dots moved in straight lines at constant speeds (Figure 4B). We then corrected for low-level motion cues (linear interpolation 'slows' the speed of individual joints as they take a more direct route) by matching the average joint velocity to the original sequence.

Experiment 3: Action discrimination

We asked participants to perform explicit discrimination between a fighting and a dancing action (Figure 5A-B). In this experiment we departed from the two alternative forced choice (2AFC) methodology by only presenting one 2.5 second sequence per trial (randomly selected between fighting and dancing). We corrected for the slightly slower motion cues in the dancing sequence by matching the average velocity between the two sequences. Participants were asked to indicate whether the action type of the presented sequence was fighting or dancing. There were upright and inverted conditions, occurring exactly as described in Experiment 1.

Experiment 4: Limb scrambling

To examine the possibility that a capacity to detect a coherent whole might lend controls an advantage in detecting BM, experiment 4 retained the BM dynamics of individual joint movements but removed coherence by temporally de-phasing the limbs (see Fig 2E-F). This manipulation was achieved by assigning to each limb a unique starting point with respect to the original sequence (compare Fig 2C with 2F). Participants were asked to select the target sequence, where limbs were intact, as opposed to the non-target

sequence, where the limbs were scrambled to varying degrees (Neri, 2009). Stimulus duration was 2 seconds.

Experiment 5: Agent scrambling

The two agents in our sequences interact in a meaningful way either through dancing or fighting, and action interpretation of one agent enhances sensitivity to the action pattern associated with the other agent (Neri et al., 2006). In the same way that point-lights within an individual generate a percept of coherent motion as a result of being commonly related to a single action sequence, so it is with 2 individuals related to one another by a common activity. If a disruption of the ability to perceive coherence causes impaired BM perception in ASD, then coherence at this higher level should be a highly sensitive measure. However, the above-detailed experiments (1-4) do not probe the ability to detect inter-agent interaction. We designed a manipulation that shifted all joints of one agent forward or backward in time relative to the other agent (Figure 2G-H), allowing us to vary the degree to which the two agents acted in synchrony with one another. Consequently, the meaningful link between one agent's actions and the other agent's actions (e.g. if one agent punches, the other agent attempts to block the punch) was lost in the scrambled sequence. Participants were asked to identify the synchronised (target) sequence (Figure 2B versus 2H). Successful discrimination was specifically dependent upon detection of inter-agent interaction and could not be achieved by relying on the cues that potentially supported previous tasks because intact body fragments, as well as full agents, were delivered by both 'target' and 'non-target' sequences (compare Figure 2A-B with 2G-H). In this experiment we also departed from the general protocol by ensuring that agents were clearly distinct from one another: all joints for one agent were bright (100% contrast) while all dots for the other agent were dark. All joints were also continuously displayed for the entire duration of the stimulus (no limited-lifetime sampling).

Experiment 6: Generic attention

Group differences in studies of BM perception in ASD could potentially be generated by differences in attentional capacities. To test for a potential role of generic attentional resources, we briefly reduced the contrast (from 100% to 50%) of three randomly selected 'target' joints on the two agents at a random time-point throughout stimulus presentation (Figure 7A-B), and asked observers to report whether the target joints were brighter (light gray) or darker (dark gray) than the background. We then varied the time period during which the change was applied and estimated threshold duration for performing this task (Figure 7C). The contrast change was well above threshold visibility; task difficulty was therefore dependent upon the capacity for sustained voluntary attention (Corbetta and Shulman, 2002) required to monitor the entire 2.5-sec sequence on every trial, so as to not miss the change when it occurs. One interval (2.5 sec duration) was presented on each trial with longer limited lifetime (250 ms). There were no noise dots, and the 16 sampling dots had longer limited lifetime (250 ms).

RESULTS

Results of paired-tests and group comparisons are shown in Table 1. Threshold measurements for experiment 1 are shown in Figure 3H: the ability to discriminate intact versus scrambled biological motion sequences is lost with fewer masking noise dots when the display was inverted upside-down (data points lie above the diagonal equality line), and the magnitude of this effect is similar for both ASD and TD groups (solid and open symbols respectively in Figure 3H).

In Experiment 2 we observed no substantial change in noise tolerance thresholds when switching from the animate (Figure 4A) to the robotic stimuli (Figure 4B) for both ASD and TD populations (data points scatter around unity line in Figure 4C), indicating that the local motion patterns specifically associated with biological movement are processed similarly by ASD and TD visual systems. In Experiment 3, which required actions (fighting versus dancing) to be discriminated from one another (Figure 5A versus 5B), clear inversion effects were similarly detected in both groups (Figure 5C). The same result was obtained for Experiment 4, where participants with ASD showed a similar susceptibility to the effects of limb-scrambling and the degree to which this was affected by inversion (Figure 6E). In Experiment 5, ASD and TD groups demonstrated comparable ability to detect inter-agent interaction and a similar degree of impairment with inversion (Figure 6F). Finally, in Experiment 6 both groups showed similar thresholds for identifying a brightness change applied to a random subset of the joints (Figure 7C).

Overall comparison of results

Finally, we considered that a subtle deficit of biological motion perception could exist which was undetected in separate experiments but which may become evident if all results were combined. We investigated this by normalising thresholds within each experiment and collating overall results. We found a non-significant trend towards poorer thresholds for both upright and inverted conditions in the ASD group ($t(128) = -1.8844$, $p = 0.062$; Figure 8A-B), but upright/inverted log-ratios were virtually identical ($t(128) = -0.2184$, $p = 0.858$; Figure 8C). The overall drop in sensitivity we measured across experiments and groups was ~1/2 log-unit, in close agreement with previous estimates (Neri et al, 2007).

DISCUSSION

We designed a battery of experiments that sought to comprehensively test the hypothesis that the ability to detect biological motion in autism is impaired. None of our experiments revealed any significant group differences. Rather, we found clear evidence of an inversion effect in several experiments for both groups, which is indicative of intact action-perception in ASD. We emphasize that the observed lack of measurable differences between TD and ASD populations is not a consequence of poor resolving power associated with our protocols: it is not that we failed to measure any effect (e.g. deficit) in either TD or ASD populations; to the contrary, we reliably measured inversion effects across several experiments, yet those measured effects were of similar magnitude for TD and ASD participants (Figure 8C).

When we combined data across our large dataset, we did find a (non-significant) trend towards a group difference (rightward-pointing arrows in Figure 8A-B). Several

possibilities might be considered to account for this suggestive result (besides the possibility that it may represent a chance finding). Visual noise theories suggest a more generalised impairment of visual perception in autism deriving from increased neural noise in the visual cortex (Simmons et al., 2009; Dinstein et al, 2010). The absence of group differences in upright tasks argues against this interpretation, although we emphasise that our findings are most specific to the question of action-perception. Another possibility is that it stems from differences in executive function between groups (see below). Finally, action processing might only be affected in autism in certain ways, so that specific experiments might be required to measure any resulting deficit. With relation to the latter possibility, we selectively examined 3 separate functions that might generate specific group differences.

First, we considered the notion that animacy detection might be impaired in ASD: some research has shown abnormal perception of 'animate' or life-like kinematics in autism (Rutherford et al., 2006; Cook et al., 2009), whilst other research has suggested that individuals with autism display atypical motor kinematics relative to a typically developing population (Cook et al., 2013; Cook et al., 2014). We did not measure any effect of joint kinematics in either group, indicating that the dynamics of individual dot movements are not critical to the detection of an overall biological motion. The possibility that life-like kinematics might contribute to group differences is therefore a moot point.

Second, we considered whether the concept of “weak central coherence” (WCC) might be important in BM perception. WCC theory proposes that individuals with autism deploy greater attentional resources to local details as opposed to global details, and are impaired at retrieving a coherent whole percept (Plaisted, 2001; Happé and Frith, 2006; Mottron et al., 2006). In Experiment 4, we utilised a manipulation that disrupted whole coherence whilst retaining animacy of individual limbs (Neri, 2009). Both groups were equally susceptible to this disruption and inversion effects were also similar (Figure 6E). Evidently, a capacity for detecting and utilising coherence was present in both groups to a similar degree. In Experiment 5 we investigated the capacity to utilise the information carried by the meaningful interaction between two agents. The associated manipulation probed coherence at a further, even more global level than integration of limbs into whole bodies (Neri et al., 2006; Luu and Levi, 2013); it should therefore be sensitive to relatively small deficits in coherence detection. However, again we found good evidence for intact processing of inter-agent communication signals (Figure 6F).

Third, we considered that knowledge of action could be a factor. Some theoretical frameworks for understanding autism, such as the “enactive mind approach” (Klin et al., 2003) or mirror neuron theory (Williams et al., 2001; Williams 2008), propose that perception is tightly linked to action-knowledge and associated top-down influences, particularly with relation to developmental processes. Such theories would predict that a capacity for action-recognition would enhance action-detection. Once again, we found no group differences for recognizing action type, and we measured inversion effects indicative of positive performance in both groups (Figure 5C). Finally, we looked for attentional differences associated with our stimuli and found no differences in capacity for sustained attention (Figure 7C).

Together, our experiments provide strong evidence for intact BM perception in autism. Importantly, by investigating different stages of the action-processing hierarchy in a single population and by manipulating a single set of stimuli in several different ways, our experimental program contains several internal controls that aid robustness to our conclusions.

Our findings are arguably at odds with the group differences reported for fMRI signals associated with BM perception (Kaiser et al., 2010), and behavioural demonstrations that infants with autism do not attend to action kinematics or show the same preference to action as matched typically developing infants (Klin et al., 2009). Differences in results between studies highlight important aspects of our findings. We measured the capacity to detect biological motion under conditions where attention to the stimuli was maximised, while Klin and collaborators (Klin et al., 2009) measured preference for attending to BM stimuli rather than a capacity to detect them. Kaiser et al (2010) also did not control for attentional effects, and these have been shown to play an important role in generating group differences for other social stimuli such as faces (Hadjikhani et al., 2007).

The issues discussed above highlight the potential importance of executive function in BM recognition. At the theoretical level, the enactive mind approach (Klin et al., 2003) proposes that the mechanism controlling attention to social stimuli is disrupted in autism, rather than a capacity to detect them at the perceptual level. From the practical perspective of experimental design, we planned our study to minimise any effects of differences in motivation or capacity to maintain attention, and our final experiment (Figure 7) suggests that we achieved our goal. However, it remained a possibility that executive function could still impact upon our results. We further factored out any residual role for executive function deficits by normalizing our upright-display measurements with corresponding inverted-display measurements. Generalized attentional deficits or limitations associated with executive function (e.g. working memory, decision making) will have equal impact on these two conditions, and would cancel out in the upright/inverted comparison. The inversion effects we consistently measured across our experimental programme therefore reflect genuine changes in perceptual sensitivity for discriminating our BM stimuli. By replicating previously reported effects (Neri et al., 2007), they also demonstrate that our approach is robust and supports accurate psychophysical threshold measurements.

Another important difference is that Klin and collaborators (Klin et al., 2009) report findings in infants, while we report on adolescents. This raises a question as to whether the capacity to detect BM might have a developmental aspect to it (Freire et al 2006), and whether we might have detected group differences had we employed a younger population. Evidently, we are unable to answer this question definitively using the results from this study, but we are not aware of any relevant published measurements and our own estimates of the inversion effect (upright/inverted log-ratios) do not correlate significantly ($p>0.05$) with age in either population over the (admittedly limited) range we tested (12-19 years). Again, any developmental model would need to disentangle the capacity for BM detection from the development of executive function, which influences experimental task compliance and utilisation in higher cognition. Given that a capacity for detecting BM is evident in very young infants (Simon et al., 2008), it would seem likely that executive function would place a bottleneck on the class of threshold measurements used in our study.

Conclusion

Our results demonstrate that individuals with ASD possess intact, functioning neural circuitry for perceptual processing of socially relevant visual signals (see also Dinstein et al. 2010): when they look at other people, under controlled well-motivated conditions, their perceptual system returns functionally intact signals for interpreting those people's actions adequately. However, it remains the case that individuals with autism may still fail to attend to those signals or may not take action upon them for the purpose of typical social interaction.

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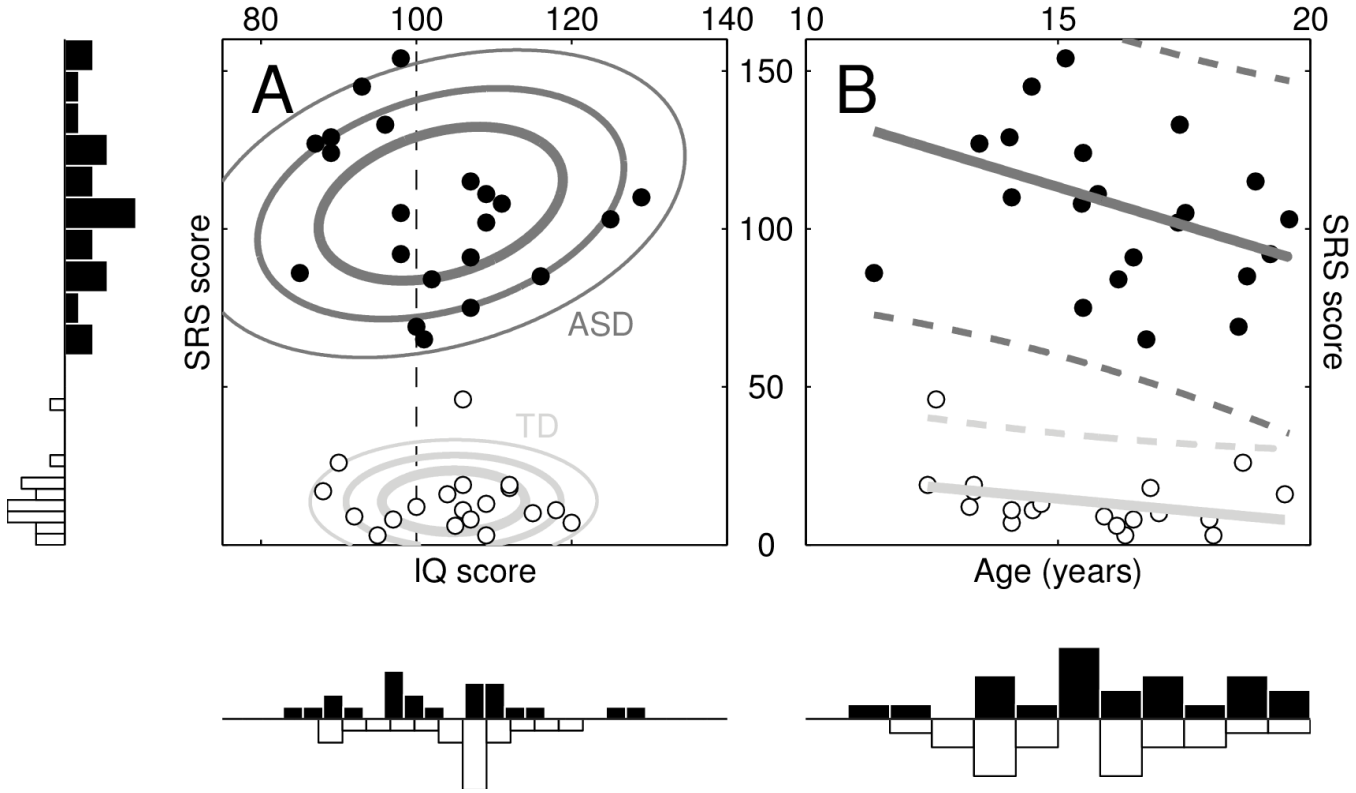

Figure 1: Autistic and control populations were matched in all respects except for autistic traits. A plots social responsiveness scale (SRS) scores on the y axis versus intelligence quotient (IQ) on the x axis. B plots SRS against age. The ASD population (solid) clearly shows higher SRS scores but equivalent IQ and age relative to the TD population (open). Ovals in A are aligned with best linear fit, their radii matching 1×, 1.5× and 2× (from thick to thin) the standard deviation of the data projected onto the fit line and the line orthogonal to it. Solid lines in B show linear fits, dashed lines mark 95% confidence intervals on the fit. Side histograms plot data distributions collapsed across corresponding axis.

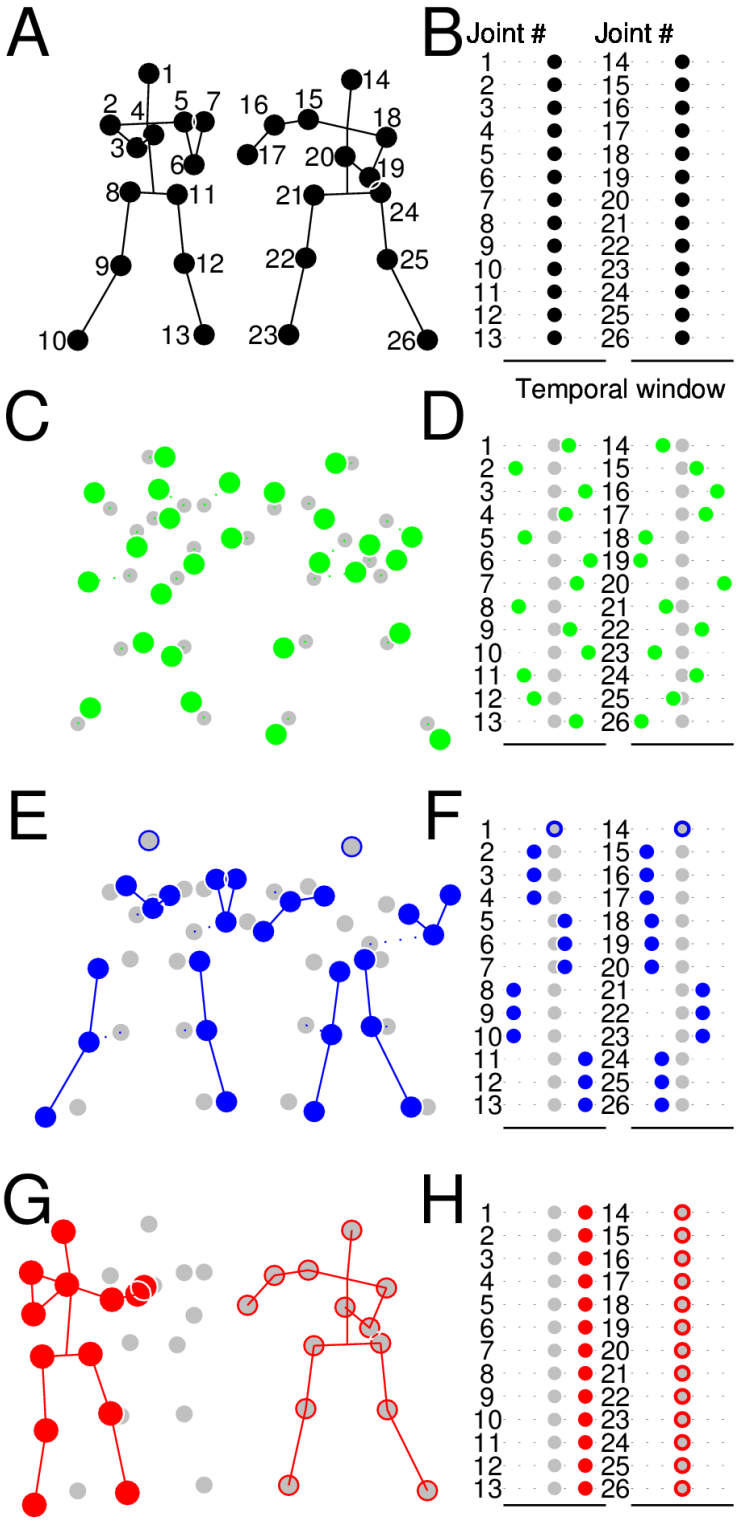

Figure 2: Selective scrambling of different stages along the action processing hierarchy. The original fighting sequence (A) was scrambled by randomly time-shifting individual joints (C-D), limbs (E-F) or agents (G-H). The three manipulations are depicted by coloured solid dots shifting away from their original trajectory (indicated by gray dots) in both first and second columns (the former in actual monitor coordinates, the latter in time coordinates) with respect to individual joints (indexed from 1 to 26 as labelled in A). Participants were asked to discriminate between intact (A) and scrambled displays (C, E, G).

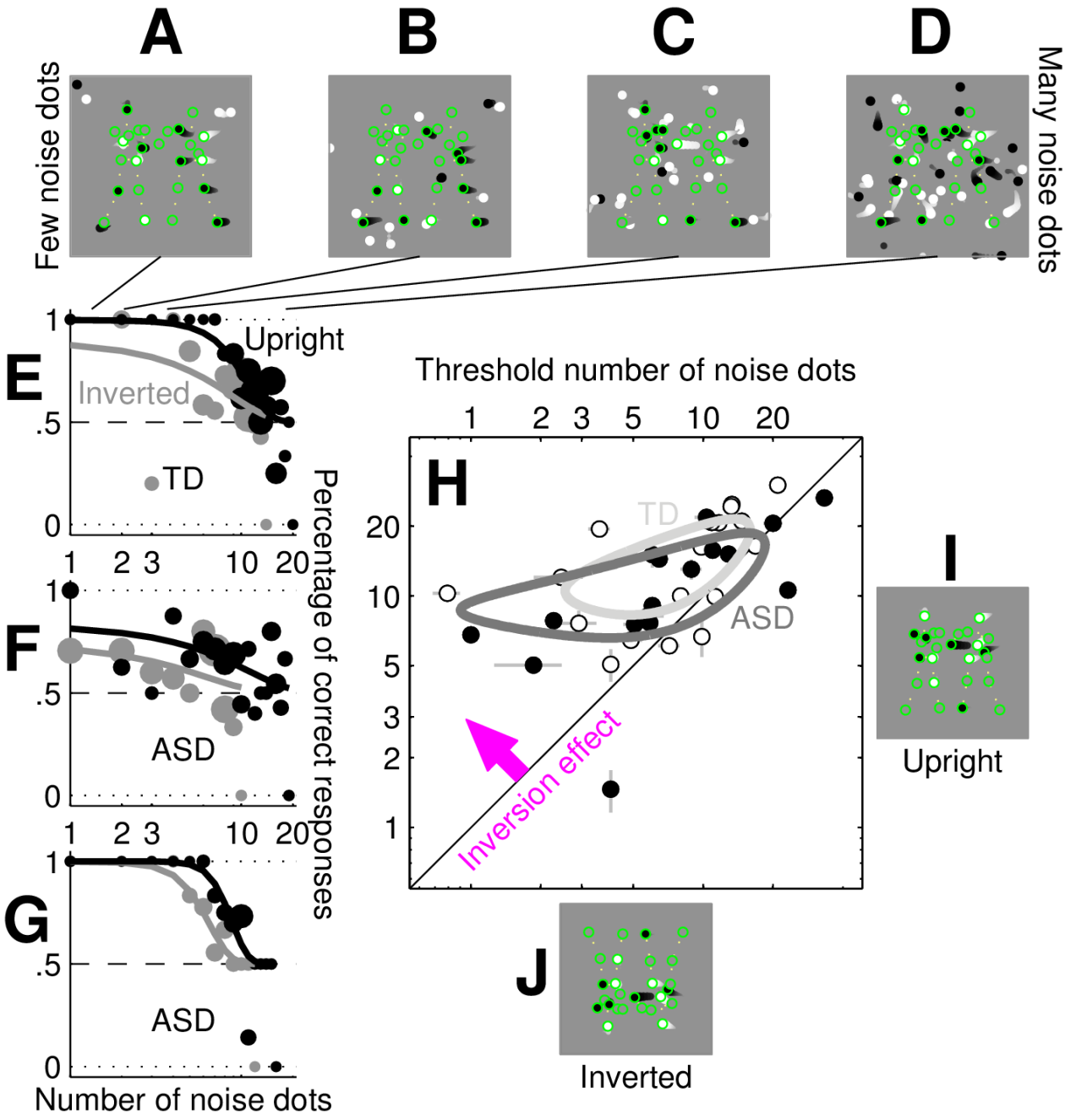

Figure 3: The disruptive effect of inversion on sensitivity to biological motion is present in both ASD and TD groups. Panels A-D demonstrate increasing levels of noise, plotted against panel E, in order to show corresponding variation in noise level. E-G show three example psyhometric functions (percent correct as a function of stimulus noise intensity) for ASD (F-G) and TD (E) participants in both upright (black) and inverted conditions (gray). F-G show variation in measurement reliability found between participants within the ASD group, whilst E demonstrates a psychometric function typically found in TD participants. H plots perceptual thresholds for upright (y axis) versus upside-down displays (inverted) across both ASD (solid) and TD (open) populations. Error bars show ±1SEM (not visible when smaller than symbol). H demonstrates an inversion effect in both groups (data points are shifted away from the diagonal equality line in the direction indicated by the magenta arrow).

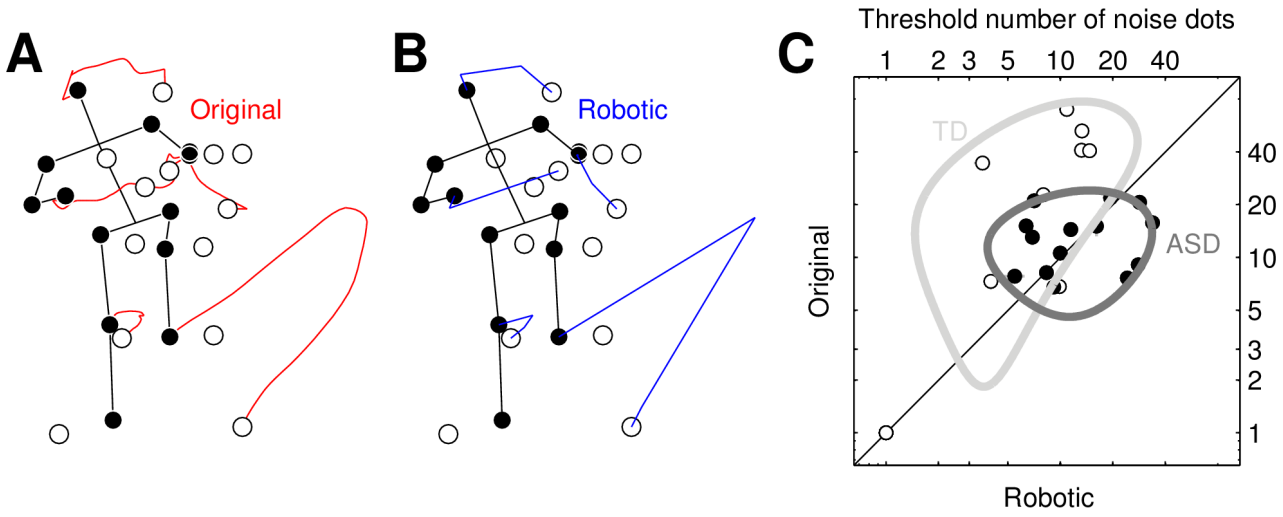

Figure 4: We modified joint trajectories (A) to move in a robotic fashion (B), and compared corresponding perceptual thresholds (x axis in C) with those obtained from the original sequence (y axis). Plotting conventions in C are similar to Figure 3H.

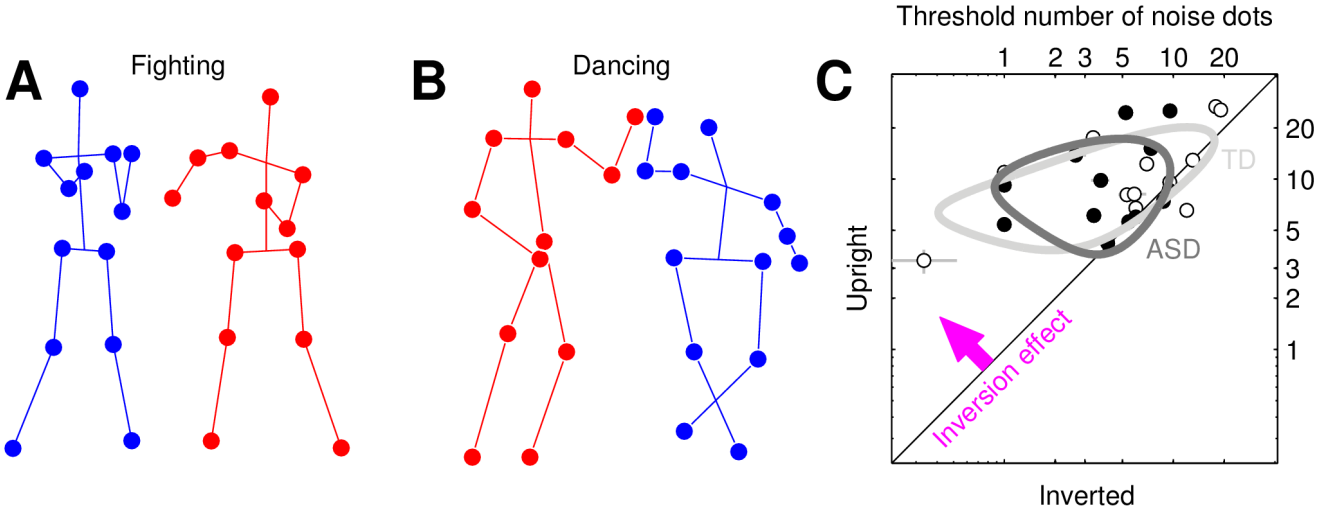

Figure 5: We asked participants to discriminate fighting (A) from dancing (B) and measured corresponding perceptual thresholds (C). Plotting conventions in C are similar to Figure 3H.

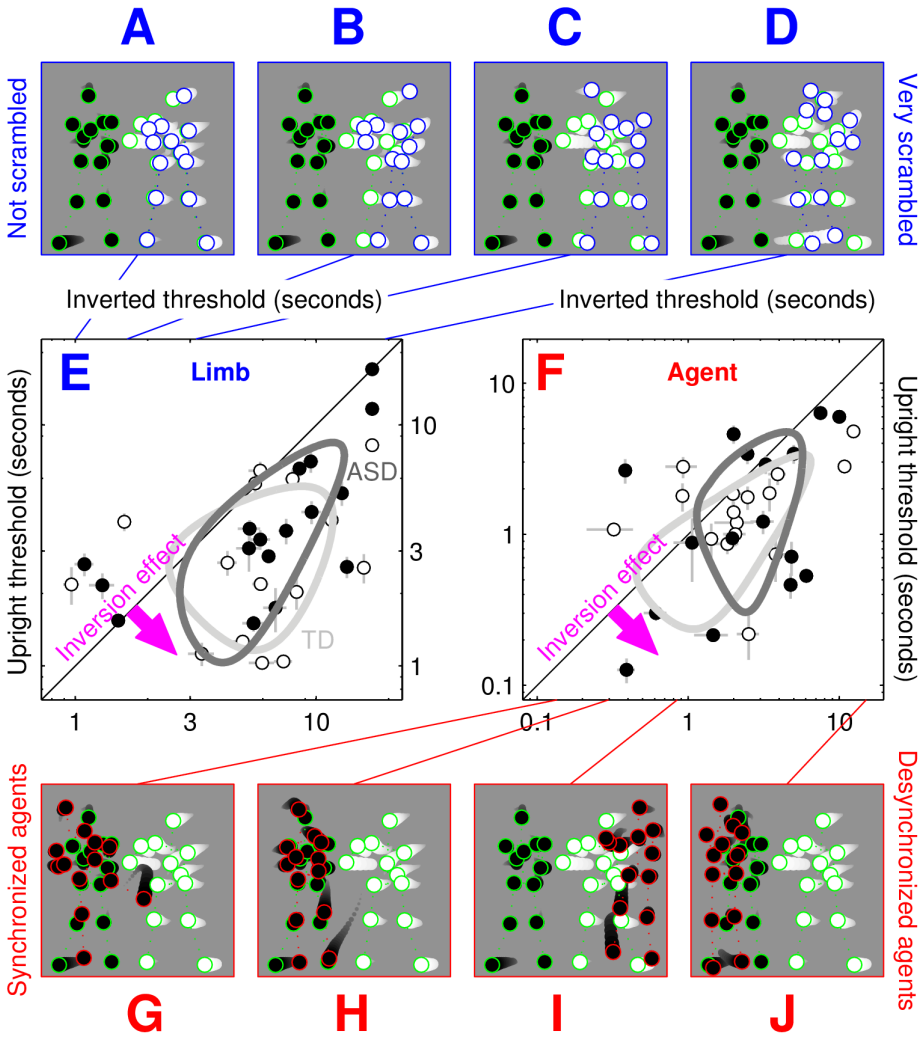

Figure 6: Inversion affects further stages of action processing in both groups. E-F plot scrambling thresholds for both ASD (solid) and TD groups (open) in upright (y axis) and inverted conditions. Icons in A-D depict varying levels of limb scrambling (increasing from left to right), G-J show varying scrambling levels of inter-agent synchronization. Plotting conventions in E-F are similar to Figure 3H.

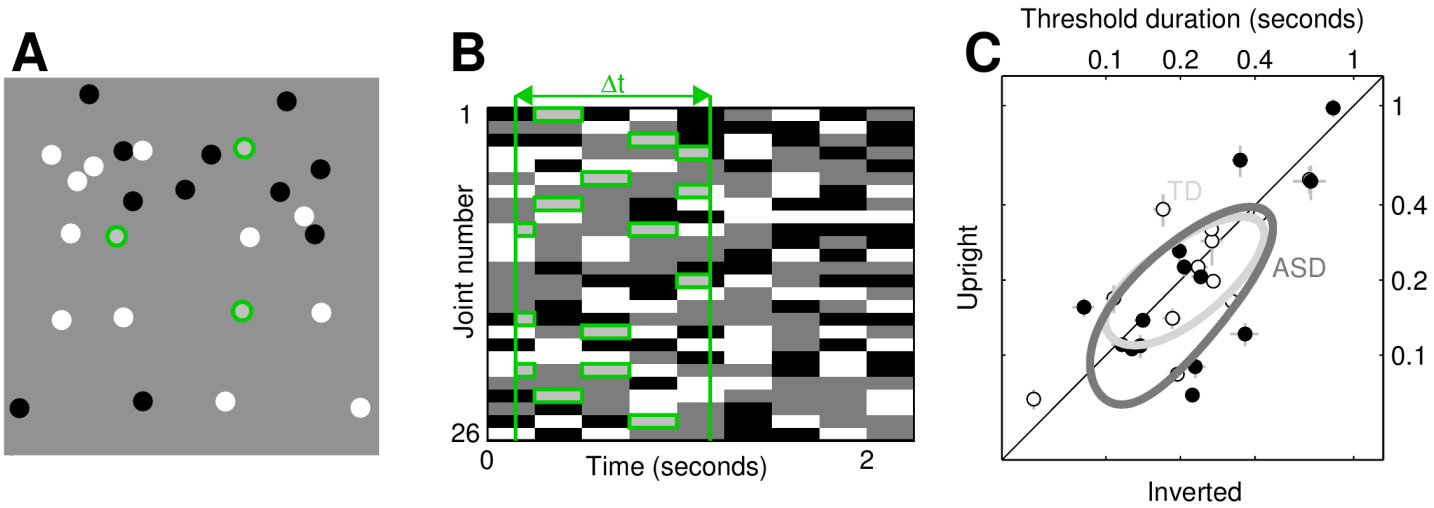

Figure 7: We probed the potential role of generic attention by reducing the contrast of three joints for a brief period of time (indicated by Δt in B) during a relatively long presentation of the fighting sequence. Participants were asked to identify whether the target joints (green outline in A-B) were "dark gray" or "light gray" (latter shown in A-B). C plots duration thresholds for judging the brightness of the modified joints (see Methods). Plotting conventions in C are similar to Figure 3H.

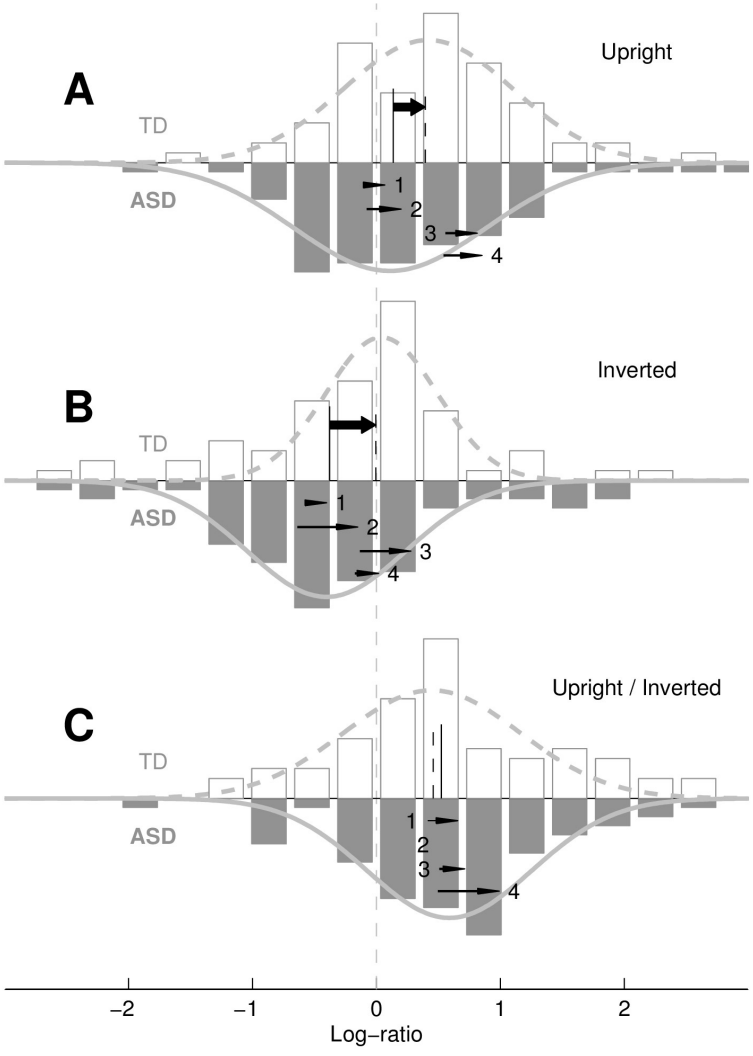

Figure 8: ASD thresholds are slightly worse than control, but this effect is not specific to action processing. A plots distribution of normalized sensitivity (larger for better performance) for ASD (solid) and TD (open) participants across 4 different experiments with upright displays. Thick arrow shows average shift from TD (vertical dotted line) to ASD (vertical solid line) across all 4 experiments; small arrows show shifts for different experiments (labelled numerically as 1 for joint scrambling, 2 for limb scrambling, 3 for agent scrambling, 4 for action recognition; no arrow is plotted when arrow length is shorted than arrow head). Smooth lines show Gaussian fits (solid for ASD, dashed for TD). B plots same for inverted displays. In both A and B, ASD sensitivity tends to be lower than TD (all small arrows point to the right). C plots upright/inverted sensitivity ratios from A-B using the same plotting conventions; when cognitive components not specific to action processing are factored out in this way, there is no longer any trend for a difference between ASD and TD populations.

Table 1 results

Experiment	Control (TD)						ASD						Group difference for upright		Group difference of log ratios	
			Paired t-test						Paired t-test				Unpaired t-test			
	Upright Mean (SD)	Inverted Mean (SD)	df	t	p	Mean log ratio	Upright Mean (SD)	Inverted Mean (SD)	df	t	p	Mean log ratio (SD)	t	P	t	p
1. Upright vs Inverted BM detection	14.59 (8.03)	9.44 (5.31)	17	3.70	0.0018	0.47 (0.82)	12.48 (6.59)	9.34 (8.23)	17	2.36	0.0297	0.46 (0.69)	0.93	0.3567	-0.04	0.9719
3 Action discrimination	11.98 (7.19)	7.94 (5.31)	14	2.96	0.012	3.43 (3.67)	10.48 (6.88)	5.75 (3.50)	14	2.36	0.0299	2.78 (2.51)	0.52	0.6053	-0.54	0.5939
4 Limb Fragments	201.92 (136.57)	426.02 (276.93)	14	3.7	0.0041	-0.47 (0.94)	299.47 (244.8)	495.74 (300.15)	14	4.51	0.0003	-0.68 (1.13)	1.16	0.2534	0.54	0.3721
5 Agent synchrony	103.54 (66.53)	198.12 (204.12)	17	-2.34	0.0337	-0.47 (0.94)	131.86 (121.36)	221.99 (173.47)	17	-2.54	0.0220	-0.68 (1.13)	0.11	0.9107	0.54	0.3721
6 Attention	14.28 (7.66)	16.32 (9.30)	14	-2.34	0.2923	na	19.70 (23.84)	25.45 (26.64)	14	-1.22	0.2793	na	0.24	0.8139	1.18	0.4163
	Animate	Linear					Animate	Linear								
2 Animacy	14.12 (10.52)	15.19 (8.51)	14	-0.67	0.5165	0.31(0.72)	15.09 (9.37)	13.1 (5.14)	14	0.8	0.4370	0.04 (0.65)	1.05	0.3026	1.38	0.1786

Table 1: Results from all 6 experiments showing that there are no differences between groups in any experiment. There is a significant difference between upright and inverted conditions in experiments 1, 3, 4 and 5.