



# Typical Use of Inverse Dynamics in Perceiving Motion in Autistic Adults: Exploring Computational Principles of Perception and Action

Shinya Takamuku <sup>†</sup>, Paul A. G. Forbes,<sup>†</sup> Antonia F. de C. Hamilton, and Hiroaki Gomi

There is increasing evidence for motor difficulties in many people with autism spectrum condition (ASC). These difficulties could be linked to differences in the use of internal models which represent relations between motions and forces/efforts. The use of these internal models may be dependent on the cerebellum which has been shown to be abnormal in autism. Several studies have examined internal computations of forward dynamics (motion from force information) in autism, but few have tested the inverse dynamics computation, that is, the determination of force-related information from motion information. Here, we examined this ability in autistic adults by measuring two perceptual biases which depend on the inverse computation. First, we asked participants whether they experienced a feeling of resistance when moving a delayed cursor, which corresponds to the inertial force of the cursor implied by its motion—both typical and ASC participants reported similar feelings of resistance. Second, participants completed a psychophysical task in which they judged the velocity of a moving hand with or without a visual cue implying inertial force. Both typical and ASC participants perceived the hand moving with the inertial cue to be slower than the hand without it. In both cases, the magnitude of the effects did not differ between the two groups. Our results suggest that the neural systems engaged in the inverse dynamics computation are preserved in ASC, at least in the observed conditions. *Autism Res* 2018, 0: 000–000. © 2018 International Society for Autism Research, Wiley Periodicals, Inc.

**Lay Summary:** We tested the ability to estimate force information from motion information, which arises from a specific “inverse dynamics” computation. Autistic adults and a matched control group reported feeling a resistive sensation when moving a delayed cursor and also judged a moving hand to be slower when it was pulling a load. These findings both suggest that the ability to estimate force information from motion information is intact in autism.

**Keywords:** autism; internal models; inverse dynamics; delayed visual feedback; velocity perception

## Introduction

Reports of abnormal motor control in people with autism spectrum condition (ASC) are common, with up to 89% co-morbidity of autism with motor problems [Green et al., 2009]. However, it has not proved easy to characterize these motor difficulties in detail. A recent review found evidence of difficulties in many different motor tasks, but also highlighted that many current behavioral tasks do not test specific computational processes [Gowen & Hamilton, 2013]. In the present paper, we specifically tested the ability of typical and autistic adults to use an inverse dynamics computation, that is, to determine force information from motion information. We first review data on internal dynamics computations, before describing the tasks we used.

## Internal Dynamics Computations

Force and motion are often mutually informative. For example, inertial force of an object can be estimated from its acceleration and vice versa according to Newton’s laws of motion. Generally, calculating motion (velocity/acceleration) information from force information (e.g., motor signals) is called the *forward* dynamics computation, whereas calculating force information from motion information is called the *inverse* dynamics computation. Importantly, both computations require estimating the mechanical dynamics of the observed system from various sensory signals.

Studies have suggested that our brain performs the two computations for motor control and sensory perception, and that the cerebellum plays a major role.

From the NTT Communication Science Laboratories, 3-1 Morinosato Wakamiya, Atsugi, Kanagawa, 243-0198, Japan (S.T., H.G.); Institute of Cognitive Neuroscience, University College London, Alexandra House, 17 Queen Square, London, WC1N 3AZ, UK (P.A.G.F., A.F.C.H.)

<sup>†</sup>Shinya Takamuku and Paul A.G. Forbes have contributed equally to this article.

Received September 29, 2017; accepted for publication April 11, 2018

Address for correspondence and reprints: Shinya Takamuku, NTT Communication Science Laboratories, 3-1 Morinosato Wakamiya, Atsugi, Kanagawa, 243-0198, Japan. E-mail: takamuku.shinya@lab.ntt.co.jp

Published online 00 Month 2018 in Wiley Online Library (wileyonlinelibrary.com)

DOI: 10.1002/aur.1961

© 2018 International Society for Autism Research, Wiley Periodicals, Inc.

Forward computations allow us to use efferent signals (force information) to predict hand movement (motion information), which are critical for adjusting actions without waiting for delayed sensory feedback [Wolpert, Ghahramani, & Jordan, 1995] and to effectively monitor actions [Blakemore, Wolpert, & Frith 1998; Christensen, Ilg, & Giese, 2011]. Several studies linked these processes to the cerebellum [Blakemore et al., 1998; Miall, Christensen, Cain, & Stanley, 2007]. The inverse dynamics computation, on the other hand, is critical when performing actions as it specifies a motor signal which generates a desired action [Kawato & Gomi, 1992; Shadmehr & Mussa-Ivaldi, 1994]. The inverse dynamics computation also estimates the dynamic forces of objects we control from their visual motion [Sarlegna, Baud-Bovy, & Danion, 2010; Takamuku & Gomi, 2015]. In vivo recordings from the cerebellum showed that Purkinje cell activity contributing to motor commands can be reconstructed from movement trajectories for both arm [Yamamoto, Kawato, Kotosaka, & Kitazawa, 2007] and eye movements [Shidara, Kawano, Gomi, & Kawato, 1993], demonstrating the core role of the cerebellum in inverse computations. The inverse computation may also be useful for extracting information from the observed motion of others, for example, it may be involved in estimating the weight of a box lifted by another person [Runeson & Frykholm, 1981; Hamilton et al., 2007] and the facilitation seen in motor learning following action observation [Mattar & Gribble, 2005]. Behaviors which involve mapping the motion of others onto our own actions, such as kinematic imitation, motor facilitation/interference, and possibly biological-motion perception, should also involve the computation in principle.

Several behavioral tasks are available to measure how people make use of the forward and inverse computations. Studies on force-field adaptation demonstrated our ability to acquire novel internal models of dynamics for predicting hand trajectories (forward dynamics) [Nanayakkara & Shadmehr 2003] and determining the motor signals which generate the desired actions (inverse dynamics) [Shadmehr & Mussa-Ivaldi, 1994; Conditt, Gandolfo, & Mussa-Ivaldi, 1997]. Grip-force-control studies revealed our ability to predict dynamic forces experienced during arm movements [Flanagan & Wing, 1997] and showed that the visual motion of objects we control contributes to the force calculation [Sarlegna et al., 2010]. Perceptions of self and object motions which are dependent on internal models can also be tested. For instance, we can examine the ability to estimate the weight of an object lifted by others [Runeson & Frykholm 1981; Hamilton et al., 2007] and the ability to use this information for our own actions [Reichelt, Ash, Baugh, Johansson, & Flanagan, 2013]. Next, we describe two perceptual tasks used in the

present study to measure participants' ability to perform the inverse computation.

The first task involved a proprioceptive illusion experienced while moving a delayed cursor—imagine moving a computer mouse with a noticeable delay between the hand action and the cursor movement. In such contexts, participants report an illusory percept of resistance to their action, almost as if the mouse is heavy. Studies have shown that a delay increases the perceived weight of a controlled object [Honda, Hagura, & Imaizumi, 2013] and changes the temporal pattern of grip-force applied to an object [Sarlegna et al., 2010]. This evidence suggests that the delay changes our internal estimate of the reaction force involved in our action. The illusion was initially assumed to reflect the discrepancy between displayed and predicted cursor motions: the latter is generated from the forward model [Honda et al., 2013]. However, when we systematically varied the cursor motion to examine the origins of the effect [Takamuku & Gomi, 2015], the strength of the resistive sensation did not correlate with the errors of cursor position, velocity, or acceleration caused by the delay. Instead, the strength correlated with the amount of exposure to the forward acceleration of the cursor. Following Newton's laws of motion, forward acceleration of a moved object correlates with its inertial reaction force. Therefore, the result suggested that the illusion occurs because the brain erroneously interprets the delayed cursor as a pulled load rather than a mere indicator of hand position and makes us perceive the cursor's imaginary inertial force which we estimate from its motion. The theory that we assume an inertial force of the delayed cursor also explains the peculiar temporal shift in grip-force pattern observed when moving a delayed cursor [Sarlegna et al., 2010]. Thus, the magnitude of the delayed-cursor illusion provides a specific measure of how much participants make use of the inverse computation in perceiving self-actions.

The second measure used in the present paper tested how people use inverse computations in perceiving the velocity of external objects. Velocity perception is biased by implied dynamics [Runeson, 1974; La Scaleia, Zago, Moscatelli, Lacquaniti, & Viviani, 2014], reflecting our sensorimotor experience [Brown, Wilson, Goodale, & Gribble, 2007]. This was quantified by Parovel and Casco [2006] using the launching stimuli traditionally used in studies of causality perception [Michotte, 1963]. Participants saw object A hit object B. Object B either moved immediately after the contact with object A (perceived as launching) or after a delay (perceived as independent). Participants judged B as faster in the launching case, and only in this case was the judged velocity of B correlated with the velocity of A. Here, the causal chain in the interaction is implicitly assumed. First, information concerning the interaction force,

which acts between the objects, is estimated from the relevant motion of object A (inverse dynamics computation). Secondly, the motion of object B, which appeared to receive the force, is predicted from the estimated force (forward dynamics computation). Finally, the prediction biases the perceived velocity of object B. In line with this idea, earlier studies suggested that the impact force is estimated from the relevant motion based on internal models obtained from everyday physical interactions with objects, such as kicking a ball [see White, 2012, for review]. A study which measured oculomotor responses showed that the motion of the hit object was predicted from the motion of the object that hit it [Badler, Lefevre, & Missal, 2010]. Additionally, how the prediction, obtained from the computations, biases the perception can be described in terms of Bayesian theories of motion perception [Weiss, Simoncelli, & Adelson, 2002] in which judgements of perceived velocity arise from Bayesian integration of observed and expected motions. Generally, the expectation, also referred to as the prior, is related to the statistical distribution of velocities in the natural world [Stocker & Simoncelli 2006]. The prior is dependent on context [overwritten by active control of the motion, Hu & Knill, 2010] and is constantly updated by experience [Sotiropoulos, Seitz, & Seriès, 2011].

In the current study, we examined a similar bias in perceived velocity associated with a visually implied inertial force. In our pilot study, we asked participants to judge the velocity of a moving hand in two contexts. In the first context, participants saw a hand pulling a toy car with a string so that the inertia of the car could influence the hand movement. In the second context, the hand and car moved along the same paths but were independent of each other as there was no string connecting them. Although the motion of the hand and the car did not differ between the two conditions, the hand was perceived to be slower when a string was drawn between the two objects to indicate that the car was pulled by the hand [Takamuku et al., unpublished]. The observed effect is again consistent with the theory that the sequence of inverse and forward computations biases our velocity perception. Namely, when the string is absent, the velocity of the hand can be judged based on information from the hand movement on the screen together with priors regarding natural hand movements. However, when the string is present, the inertia of the car implied by its visual motion (estimated based on inverse dynamics computation) forms an expectation that the hand will decelerate due to the resistive force (predicted based on forward dynamics computation), and the integration of this expectation with the visual information reduces the perceived velocity. Further tests showed that this effect disappeared under stroboscopic conditions in which the encoding of the

car's motion was disturbed. The effect also varied according to phase delay between the motion of the hand and the car (see Section 1 in Supplementary data for both results). These results confirmed that the effect does not merely depend on the cue (string) which indicates whether or not the inertial force applies to the hand. Rather, the effect also depends on the motion of the car, the signal essential for the inverse computation of the inertial force applied to the hand. Based on this evidence, we used the difference in perceived velocity of the hand between the two conditions as another index of the inverse computation.

### *Internal Dynamics Computations in Autism*

The studies reviewed above made it clear that forward and inverse computations are important for motor control and motion perception and have been strongly linked to the cerebellum. There are several reasons to suppose that the inverse dynamics computation might be different in autistic people, based on neural systems, studies of motor control and biological motion processing. We briefly summarize each in turn.

Consistent evidence of cerebellar abnormalities have been reported in autistic people, such as Purkinje cell loss in the vermis and cerebellar hemispheres [Bailey et al., 1998; Kemper & Bauman, 1998; Ritvo et al., 1986; Whitney, Kemper, Bauman, Rosene, & Blatt, 2008] and abnormal volume of regions [D'Mello, Crocetti, Mostofsky, & Stoodley, 2015; Hashimoto et al., 1995; Marko et al., 2015; Murakami, Courchesne, Press, Yeung-Courchesne, & Hesselink, 1989]. There are also many reports of motor difficulties [Manjiviona & Prior, 1995; Green et al., 2009; Cook, Blakemore, & Press, 2013] with some researchers claiming a specific "autism motor signature" [Teitelbaum, Teitelbaum, Nye, Fryman, & Maurer, 1998; Jansiewicz et al., 2006; Anzulewicz, Sobota, & Delafield-Butt, 2016].

These findings have led researchers to seek evidence for potential differences in forward and inverse computations in autistic people. So far, studies on forward dynamics computation have produced mixed results. Sensory attenuation of tickling sensations, which is believed to reflect the forward computation carried out in the cerebellum [Blakemore et al., 1998], was found to be intact in ASC [Blakemore et al., 2006]. Initial reports on pursuit eye movements [Takarae, Minshew, Luna, Kriskey, & Sweeney, 2004; Takarae, Minshew, Luna, & Sweeney, 2007; Takarae, Luna, Minshew, & Sweeney, 2008] found reduced gain in open-loop and closed-loop control of pursuit, the latter considered to involve prediction of object motion. However, later studies [Aitkin, Santos, & Kowler, 2013; Ego et al. 2016], which specifically tested anticipatory aspects of pursuit [e.g., Becker & Fuchs, 1985], failed to find group

differences. There are reports of both normal [Gowen & Miall, 2005] and abnormal [David et al., 2009; Mosconi et al., 2015] grip force control in tasks which involve predicting the motion of controlled objects. One study [Schmitz, Martineau, Barthélémy, & Assaiante, 2003] reported increased latency in anticipatory adjustment during an unloading task. Thus, it remains unclear whether forward dynamic computations are typical or atypical in people with autism.

There are also several studies which have (sometimes indirectly) examined inverse dynamic computations in autism. Abnormalities in the inverse computation of motor commands for producing desired motion trajectories would result in atypical kinematics of motion trajectories. Several studies have reported atypical kinematics both in eye [Takarae et al., 2004; Glazebrook, Gonzalez, Hansen, & Elliott, 2009; Schmitt, Cook, Sweeney, & Mosconi, 2014] and arm [Glazebrook et al., 2009; Cook et al., 2013] movements. However, these could also be attributed to differences in other aspects of motor control such as increased noise, motion planning, and optimization.

Studies on motor adaptation provide a unique opportunity to examine differences in internal computations of dynamics by introducing changes in sensorimotor dynamics (i.e., relation between force and motion) [Shadmehr & Mussa-Ivaldi, 1994]. In such studies, participants typically move their eyes or arm to a series of targets with either a visual transformation or a force field applied to the movement. Both learning rates and the participants' behavior when the transformation is removed (aftereffect) can be measured which allow us to examine how internal models for the inverse computation are acquired and encoded. Gidley-Larson, Bastian, Donchin, Shadmehr, and Mostofsky [2008] found no differences between typical and autistic children in adaptation to prisms, visual rotations, or force fields when comparing the learning rates or aftereffects. While this suggests intact abilities in the acquisition and employment of the internal models, studies on saccade adaptation [Johnson, Rinehart, White, Millist, & Fielding, 2013; Mosconi et al., 2013] have suggested otherwise reporting abnormalities in learning rate as well as the level of adaptation in ASC. It should be noted, however, that these abnormalities may also reflect differences in other aspects of motor adaptation. For example, they could reflect differences in the ability to acquire a novel forward model which can be used to reshape the inverse model based on internal simulations [as modeled by Jordan & Rumelhart, 1992].

As for force-field adaptation in reaching movements, Haswell, Izawa, Dowell, Mostofsky, and Shadmehr [2009] found, that autistic children displayed a stronger tendency to represent forces in intrinsic (proprioceptive) rather than extrinsic (visual) coordinates. Furthermore,

this difference correlated with impairments in social functioning and imitation. Similarly, Marko et al. [2015], found that autistic children were less sensitive to visual perturbations but more sensitive to proprioceptive perturbations during force field adaptation. This tendency was negatively correlated with anterior cerebellar volume. The difference in visual sensitivity suggests a deficit in the ability to extract information about applied forces from the observed motion of the perturbed arm. This process involves an inverse dynamics computation based on visual motion. The presumed deficit also explains the difference in the internal representation of the force field. However, it is not clear if this deficit is task-specific or whether it also applies to other cases where people use visual information to estimate the dynamics of objects.

Another line of evidence which is relevant to the inverse computation is the possibility of atypical biological motion processing in autism. Several processes which are considered to involve direct mapping of observed motion to self-action have also been described as abnormal in autism. These include motor interference [Cook, Swapp, Pan, Bianchi-Berthouze, & Blakemore, 2014; Théoret et al., 2005], imitation of action kinematics [see Gowen, 2012 for review], and biological motion perception [Blake, Turner, Smoski, Pozdol, & Stone, 2003; Tardif, Lainé, Rodriguez, & Gepner, 2007; Koldewyn, Whitney, & Rivera, 2010; Cook et al., 2014; Uono, Sato, & Toichi, 2014; Shah, Bird, & Cook, 2016]. However, some of these results are controversial [Gowen, Stanley, & Miall, 2008; Jones et al. 2011; Cusack, Williams, & Neri, 2015].

To summarize, current evidence on the use of forward and inverse dynamics in people with autism is very mixed. One likely reason is that many of the tasks involved multiple processes and may have failed to specifically tap into the computational process [Gowen & Hamilton, 2013]. Critically, in most cases, input to the internal models, such as the internal motor signal or the planned motion trajectory, was not observed and the computation was only assumed to underlie the observed behavior (indirect output). Furthermore, the normality of the computation was tested by evaluating performance in a given task. Therefore, the task could have been performed using different processes which do not use the internal computation. Our aim in the present study was to provide a more focused test of the use of inverse dynamics computations in autism, using the two implicit measures detailed above. Importantly, both effects were confirmed to be induced by the visually provided motion signals.

#### *Overview of Current Study*

Our study measured the use of inverse dynamics in autistic adults using the two above-mentioned tasks in

which a visually implied inertial force changes our action perception. The first task measured the perception of a resistive sensation caused by moving a delayed cursor [Takamuku & Gomi, 2015]. This examined whether the ability to perceive a visually implied *force* (inertial force) from a cursor *motion* (acceleration) was intact. The second task measured participants' velocity perception of a moving hand which was either pulling (dynamics present), or being followed (dynamics absent), by a toy car. This task had an advantage over the launching stimuli paradigm used by Parovel and Casco [2006] because the influences of motion interaction, the effect of surrounding motion signals on the velocity perception, could be excluded. As detailed below, the two conditions in the car stimuli were matched for motion interaction, which is important given previous reports of abnormal local motion interaction/integration in autism [Foss-Feig, Tadin, Schauder, & Cascio, 2013; Manning, Tibber, Charman, Dakin, & Pellicano, 2015].

We hypothesized that, if people with autism do not make use of inverse dynamics computations in the same way as neurotypical people, they may show a smaller resistance illusion in the delayed cursor task and a smaller difference in perceived velocity between the critical conditions in the car task. Conversely, if these computations are typical in autistic people, then equivalent results should be seen in both groups.

## Methods

### Participants

Twenty-seven adults with ASC (24 males) and 26 neurotypical (NT) adults (21 males) participated in the two experiments. The groups were matched for age, gender, and IQ (see Table 1). All participants in the ASC group had a diagnosis of either Asperger Syndrome or autism from an independent clinician, not linked to our research group.

To give more detail on participant's diagnosis, all participants in the ASC group completed an ADOS in our lab with a trained tester. We note that the sensitivity of the ADOS in adults with high IQ is rather low [Bastiaansen et al., 2011] and thus we did not include or exclude participants based on ADOS scores. In our sample, eight participants met the ADOS classification for autism, 11 for autism spectrum, and eight did not meet the classification for either autism or autism spectrum. All of those who did not meet the overall cut-off for autism spectrum reached the cut-off for autism spectrum on either the Communication subscale or the Reciprocal Social Interaction subscale, and all had a clear diagnostic history from an independent clinician. Two participants were also diagnosed with ADHD, and

**Table 1. Participant Details**

	NT (N = 26)		ASD (N = 27)		<i>t</i> test
	Mean (SD)	Range	Mean (SD)	Range	<i>p</i> value
Age (years)	32 (9)	19–58	34 (10)	19–52	.58
Fullscale IQ	115 (12)	93–149	117 (13)	86–152	.53
Verbal IQ	116 (11)	96–150	118 (14)	91–155	.52
Performance IQ	110 (14)	80–136	112 (13)	80–132	.57
ADOS: total			9 (3)	4–17	
ADOS: communication			3 (2)	0–6	
ADOS: social interaction			6 (2)	2–11	
Gender	5F; 21M		3F; 24M		
Handedness	2L; 24R		3L; 24R		

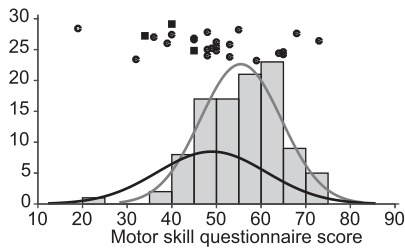
Mean ( $\pm$ SD) scores for age, IQ, and ADOS are provided.

3 also had a dyspraxia diagnosis. All participants had normal or corrected to normal vision. They gave informed consent to take part in the study, which was approved by the local ethics committee.

The autistic participants in our sample also completed a motor skill questionnaire. This was closely based on the developmental coordination disorder questionnaire [DCDQ: Wilson, Kaplan, Crawford, & Roberts, 2007], with each question adapted to suit self-report by adults. Participants had to rate the extent to which a series of fifteen statements applied to themselves on a 5-point Likert scale (e.g. “I can throw a ball in a controlled and accurate fashion”, “I can easily avoid bumping into people in a crowded room or on public transport”; see section 2 in Supplementary data for the full list of statements). The mean [SD] score of our autism sample was 49.0 [ $\pm$ 12.2] on the motor skill questionnaire (min score = 15, max score = 75; note the score of one participant was missing from the autism sample). When we compared the scores of our autism sample to 103 neurotypical participants (37 male; mean [SD] age: 33 [ $\pm$ 11] years, range 18–62 years), the neurotypical participants scored significantly higher, mean [SD] = 55.5 [ $\pm$ 9.1],  $t_{127} = 3.03$ ,  $p = .003$ , 95% CI [2.26, 10.8] but there was still substantial overlap between the groups (See Fig. 1).

### Design of Delay Perception Experiment

In the delay perception task, we examined whether participants reported a resistive sensation when moving a delayed cursor, an illusory sensation shown to depend on our inverse dynamics computation [Takamuku & Gomi, 2015]. The participants moved a digitizer on a pen tablet (Wacom, Intuos4XL) to move a cursor shown on a horizontal LCD display (top left panel of Fig. 2). The display was placed approximately 18 cm above the tablet on a wide wooden board which occluded the forearm of the participants who sat on an

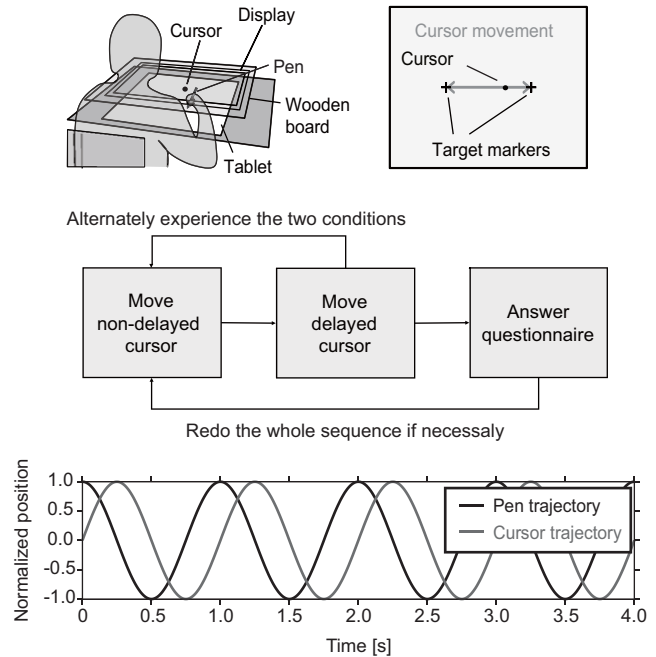


**Figure 1.** Motor skill questionnaire data. The gray line and bars show the frequency and distribution of scores for 103 neurotypical participants on the motor skill questionnaire [adapted from the DCDQ; Wilson et al., 2007]. The blackline is the distribution of the scores for the autism sample and the black dots and squares show the individual scores for each autistic participant in our sample ( $n = 26$ ; one score is missing). Black squares show data from participants with Dyspraxia.

adjustable chair. The task was to move the cursor back and forth between two markers in time with periodic beeps (top right panel Fig. 2). Participants first experienced the nondelayed (green) cursor for 30–60 s until they had adapted to the rhythm of the beep. The cursor then changed to the delayed (blue) cursor and participants were reminded to keep in rhythm with the beep. The delay was a 250 ms visual feedback delay which corresponded to  $90^\circ$  of phase delay as illustrated in the bottom panel of Figure 2. This phase delay was found to induce the strongest resistive sensation [Takamuku & Gomi, 2015]. After approximately 20–30 s the cursor was changed back to the nondelayed (green) cursor. Participants then experienced the nondelayed cursor for approximately 20–30 s before it was switched to the delayed (blue) cursor. This process was then repeated so that all participants experienced the delayed and nondelayed cursor at least three times each. Movement frequency of the cursor was specified as 1 Hz by periodic beeps, and we waited until the participants adapted to the rhythm under each condition. The adaptation to the rhythm was checked by observation during the experiment, and later confirmed based on recorded trajectory. Averaged normalized error of movement cycle within the duration at which the trajectory was most stable (5 s time window with highest autocorrelation with lag of 1 s) was  $3.0 \pm 0.4\%$  for the TD group and  $3.14 \pm 0.6\%$  for the ASC group.

After completing the motion sequence, participants answered a questionnaire referring to differences in the sensations experienced during moving the two cursors (i.e., comparison between blue and green cursors). Participants were allowed to repeat the motion sequence after having read the questions if they were unsure about their answers. The questionnaire asked the extent to which they agreed with three statements. The extent of agreement was represented on a seven-point Likert Scale (“strongly agree” being 3 points, “strongly

Does the participant feel the inertia of a delayed cursor?



**Figure 2.** Setup, stimuli, and procedure of the delay perception experiment. Top left, top right, and middle panels show setup, screen image, and procedure of the experiment, respectively. Bottom panel illustrates how the delayed cursor moved in relation to the pen.

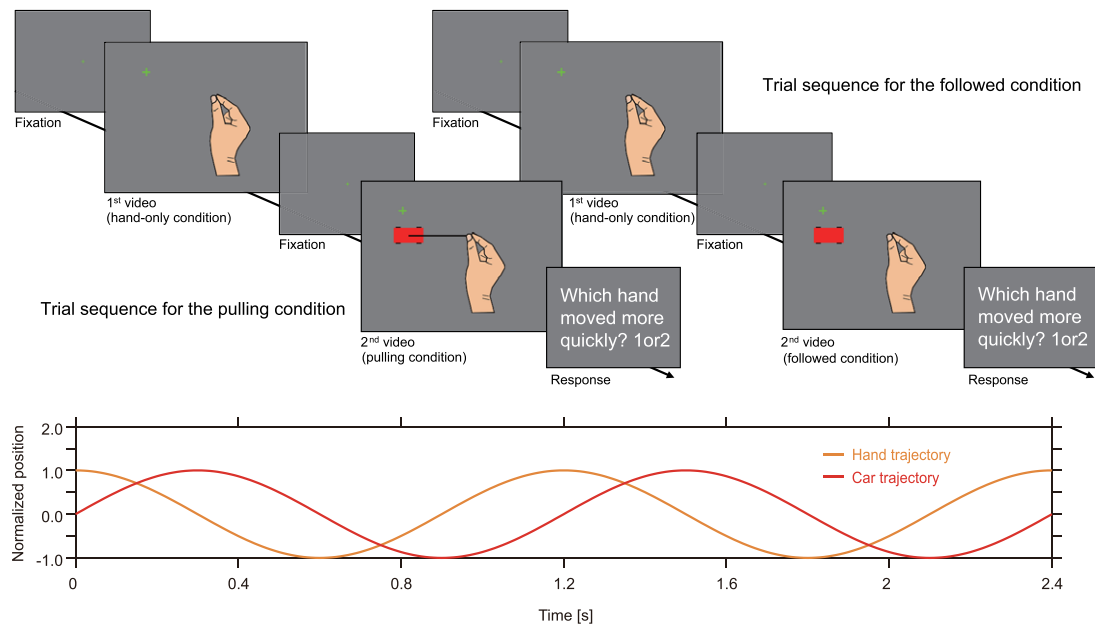
disagree” being  $-3$  points, and “unsure” being 0 points). The instructions were as follows.

Please choose the description that best explains the sensation you experienced during moving the blue cursor compared to when you moved the green cursor.

1. I felt resistance to the pen movement when moving the blue cursor.
2. The motion of the blue cursor had larger delay from the pen movement
3. The hand holding the pen felt warmer when moving the blue cursor

The first question, which was of our main interest, examined whether the participants experienced the illusory resistive sensation. The second question checked whether the participants noticed the visual feedback delay. The third statement was a control statement to confirm that they did not blindly agree or disagree to all the statements. Since neither normality, symmetry, nor equality of variance between groups could be assumed for the distribution of the scores, a sign test was used to examine whether the scores obtained for each question and group are biased toward either agreement or disagreement, and the Brunner-Munzel test [Brunner & Munzel, 2000] was used for comparing the scores between the groups.

Does the participant show bias in velocity perception caused by visually implied inertia?



**Figure 3.** Design of the velocity perception experiment. Top panel indicates sequence of typical trials for the pulling (left) and followed (right) conditions. Cropped images are shown for the stimuli used for the hand-only (control), followed, and pulling conditions to increase visibility. Note that the only difference between the pulling and followed conditions is the string between the car and the hand. Bottom panel illustrates how the car moves relative to the hand in the shown movies. Movies of the stimuli are provided as Supplementary videos S1–S3.

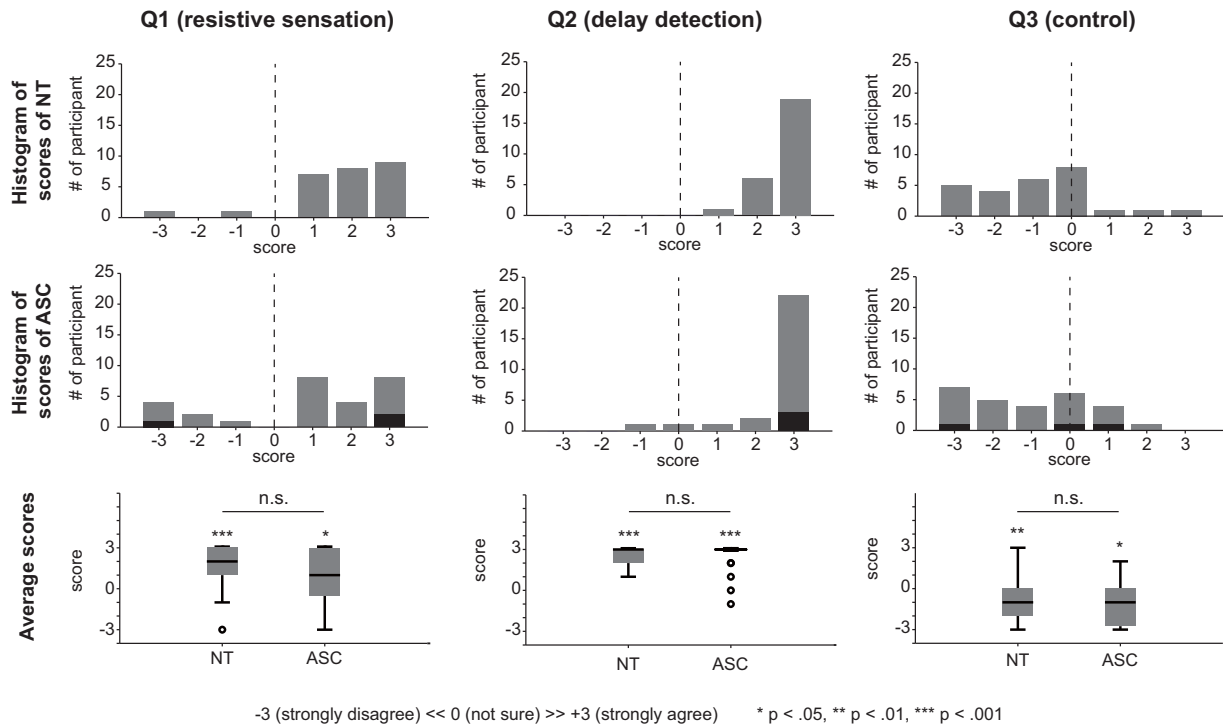
### Design of Velocity Perception Experiment

The velocity perception experiment examined whether participants experienced biases in velocity perception associated with a visually implied inertial force. Here, participants sat in front of a laptop placed approximately 57 cm from their eyes. They were told “you will see videos of a hand either moving by itself, carrying a heavy red car with a stretchable piece of string, or moving while followed by a red car.” Then, they saw three-dimensional computer graphics movies illustrating the situation of each condition (Supplementary videos S4–S6), to obtain an unambiguous interpretation of the stimulus videos.

In the experimental trials, participants observed videos of a hand moving left-to-right and back across the screen while fixating on a fixation point (green cross). The trajectory of the fingertip was sinusoidal, 1.5 cm below the fixation point, and 6.5 cm wide. The hand moved either by itself (hand-only condition), pulled a red car (pulling condition), or was followed by a red car (followed condition), snapshots of each stimuli are shown in the top panel of Figure 3. The car always traced the trajectory of the fingertip with a phase delay of 90° (300 ms) as illustrated in the bottom panel of Figure 3. The only difference between the pulling and followed conditions was the existence of a black line which connected the hand and the car. Movies of the stimuli are provided as Supplementary videos S1–S3.

Changes in perceived hand velocity, caused by the pulled and following cars, were measured by the method of constant stimuli. Namely, in each trial, participants observed the hand motion of the comparison condition and the standard condition and selected the one which appeared to move with larger velocity (2AFC) by pressing either 1 (for the first video) or 2 (for the second video) on the keyboard. The exact instruction was “Please select the video in which the hand was faster, that is, video in which hand passed below the green cross with larger velocity (larger maximum velocity).” In the standard condition, the hand moved with a movement cycle of 1.2 s, either with a pulled car or a following car. In the comparison condition, the hand moved by itself with a movement cycle of either 1.05, 1.12, 1.17, 1.2, 1.23, 1.28, or 1.35 s. Each standard condition was compared with each comparison condition 16 times. The order of the conditions as well as the order of the standard and comparison trials were both randomized.

For data analysis, we plotted the relation between normalized movement frequency (movement frequency of the hand in the comparison condition normalized by that of the standard condition) and selection probability (the probability that the hand in the comparison condition was selected to have a greater velocity than the standard condition) for each condition, and fitted a logistic psychometric function to the plots of each



**Figure 4.** Result of delay perception experiment. Top and middle row show histograms of scores of NT and ASC groups, respectively. Black bars in the ASC histogram indicate data from participants with Dyspraxia. Bottom row shows box plots of scores for each group. Left, center, and right column show results for questions 1, 2, and 3, respectively. All questions resulted in scores significantly larger or smaller than 0. Significant difference between groups was never detected.

standard condition. From this, we obtained the point of subjective equality (PSE), the normalized movement frequency at which selection probability equals 50%, for each standard condition, and the just-noticeable-difference (JND) calculated as  $|x_{75} - x_{25}|/2$ . Participants with JND exceeding the parameter range examined in the study (i.e.,  $JND = > |x_{\max} - x_{\min}|/2$ ) were excluded from the analysis due to their low ability in distinguishing the hand velocity and the resulting low reliability in estimation of their PSE as well as JND. For the remaining participants, a two factor ANOVA was applied to the PSEs to examine the effects of the visual condition, the group, and their interaction. Finally, we directly compared the PSEs of the pulling condition and the followed condition within each group to examine the effect of the visually implied inertia on our velocity perception as the second index of the inverse computation.

## Results

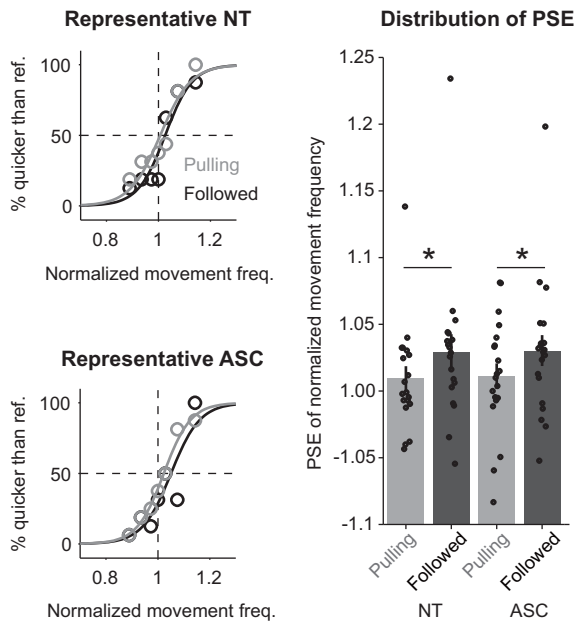
### Delay Perception

In the delay perception task, participants were asked for their agreement with three statements about their perception of a delayed cursor, and Q1 indexed their experience of inertia. Figure 4 shows histograms (top and

middle row) and box plots of the scores (bottom row) for the 3 questions for the two groups. Positive scores indicate that the participant agreed with the statement, whereas negative scores indicate that they disagreed. As clearly shown in the figure, the majority of the participants in the NT group agreed with the statements which probed their experience of the illusory resistive sensation (Q1) and their detection of the visual feedback delay (Q2); whereas most participants disagreed with the control statement (Q3). Interestingly, this was also the case for the ASC group. Although three of our ASC participants had dyspraxia, we found no major difference in their hand motion trajectories (averages and standard deviations of movement width and cycle were all within 2SD of the distribution of the control group) and therefore included them in our analysis.

Median scores for Q1 was significantly larger than zero, not only for the NT group ( $z = 4.12$ ,  $p < .001$ ,  $r = 0.81$ ), but also for the ASC group ( $z = 2.31$ ,  $p = .021$ ,  $r = 0.44$ ). Using the Brunner–Munzel test [a generalized Wilcoxon Test, see Brunner & Munzel, 2000], we did not observe a significant difference of the scores between the two groups ( $W^{BF} = -1.45$ ,  $p = .154$ ,  $p(X_{NT} < X_{ASC}) + p(X_{NT} = X_{ASC})/2 = 0.39$ ). This was also the case for the second question which examined whether they detected the visual delay. Again, median of scores for the two groups were both significantly larger than





**Figure 5.** Result of velocity perception experiment. Top left and bottom left panels show psychometric functions for representative NT and ASC, respectively. Right panel shows average PSE for each group and condition. Each error bar denotes standard-error. Two-factor ANOVA detected significant effect of visual condition, but neither the effect of group nor visual condition-group interaction was significant. PSE of the pulling condition was significantly smaller than that of the followed condition in both groups.

zero (NT:  $z = 4.90$ ,  $p < .001$ ,  $r = 0.96$ , ASC:  $z = 4.51$ ,  $p < .001$ ,  $r = 0.87$ ), and there was no significant difference between the groups ( $W^{BF} = 0.49$ ,  $p = .625$ ,  $p(X_{NT} < X_{ASC}) + p(X_{NT} = X_{ASC})/2 = 0.53$ ). As for the third question, which was the control question, median of scores for the two groups were both significantly smaller than zero (NT:  $z = -2.59$ ,  $p < .01$ ,  $r = -0.51$ , ASC:  $z = -2.18$ ,  $p < .029$ ,  $r = -0.42$ ), and did not significantly differ between the two groups ( $W^{BF} = -0.32$ ,  $p = .748$ ,  $p(X_{NT} < X_{ASC}) + p(X_{NT} = X_{ASC})/2 = 0.47$ ). Total time in which participants engaged in the cyclic movement during the task also did not differ between the two groups (TD:  $2.46 \pm 0.49$  [min], ASD:  $2.28 \pm 0.67$  [min],  $t_{51} = 1.11$ ,  $p = .27$ ). Excluding the participants with dyspraxia or those with ASD did not have any major effect on the result. Namely, all biases in the scores remained significant and there was no significant difference in scores between the two groups.

### Velocity Perception

Seven participants within each group were excluded from the analysis due to low ability in distinguishing the hand velocity (criteria explained in the method section). The final group of 20 ASC and 19 TD participants did not differ in age or IQ. Left panel of Figure 5 shows

results for representative participants of each group (upper panel: NT, bottom panel: ASC). The plots indicate the relationship between normalized movement frequency and selection probability, and the curves indicate logistic psychometric functions fitted to the plots (gray: pulling condition, black: followed condition). The right panel in Figure 5 shows the means of the PSEs for each group and condition (left: NT, right: ASC). We found a significant effect of visual condition ( $F_{1,37} = 11.4$ ,  $p < .002$ ,  $\eta_p^2 = 0.24$ ) on the PSE, but neither the effect of group ( $F_{1,37} = 8.92 \times 10^{-3}$ ,  $p = .925$ ,  $\eta_p^2 = 2.41 \times 10^{-4}$ ) nor interaction between visual condition and group ( $F_{1,37} = 3.55 \times 10^{-3}$ ,  $p = .953$ ,  $\eta_p^2 = 9.59 \times 10^{-5}$ ) was significant. Importantly, PSE for the followed condition was significantly larger than that of the pulling condition, not only in the NT group ( $t_{18} = -2.49$ ,  $p = .023$ ,  $d_z = -0.57$ ), but also in the ASC group ( $t_{19} = -2.29$ ,  $p = .033$ ,  $d_z = -0.51$ ). This means that both groups of participants showed the velocity perception bias, the index of the inverse computation.

We also examined the magnitude of the JNDs within the sample of participants who showed adequate performance, and found that neither the effect of visual condition ( $F_{1,37} = 2.50$ ,  $p = .123$ ,  $\eta_p^2 = 0.06$ ), group ( $F_{1,37} = 0.35$ ,  $p = .56$ ,  $\eta_p^2 = 9.47 \times 10^{-3}$ ), nor the interaction between those two factors ( $F_{1,37} = 2.68 \times 10^{-2}$ ,  $p < .871$ ,  $\eta_p^2 = 2.03 \times 10^{-4}$ ) was significant. Namely, we did not find any difference in the ability to distinguish the hand velocities between the two groups.

### Inverse Dynamics and Self-Reported Motor Skills

In our autism sample, we found no significant correlation with self-reported measures of motor skills and the measures of inverse dynamics we tested ( $R = -0.05$ ,  $p = 0.81$  for correlation with the score of Q1 in delay task and  $R = 0.25$ ,  $p = 0.30$  for the difference in PSE in velocity perception task; see section 3 in Supplementary data).

## Discussion

Autistic individuals may have difficulties in some aspects of motor control, motor learning, and in the processing of biological motion. One common factor underlying these skills is the inverse dynamics computation, so the current project aimed to specifically test whether this computation is aberrant in autism. We used two perceptual tasks which acted as an index for the inverse dynamics computation in a sample of autistic adults and a matched neurotypical sample. In both tasks, performance of the neurotypical and autistic adults was similar suggesting the reliable use of the inverse computation in both cases.

Our first experiment examined the feeling of resistance experienced while moving a delayed cursor. Here, our main interest was whether autistic participants perceive the inertial force implied by the delayed cursor, the sensation which is considered to depend on the inverse computation [Takamuku & Gomi, 2015]. We found that the majority of autistic participants experienced the resistive sensation, and there were no significant differences between the scores of the autistic and neurotypical participants. Additionally, we found that autistic participants were comparable to the neurotypicals in detecting the visual feedback delay; again, there were no significant differences between the two groups. This is consistent with earlier work [Fuentes, Mostofsky, & Bastian, 2011] which found that autistic individuals have no deficit in comparing hand positions estimated from visual and proprioceptive feedback. One may argue that there could be some general difference in answering questionnaires which could have hidden potential differences between the groups. For example, if autistic individuals are generally more likely to agree with a given statement, this may have hidden deficits in delay detection as well as the inverse computation. However, this is unlikely since both groups gave comparable answers on the control statement.

Our second experiment examined biases in the perceived velocity of a moving hand caused by the estimation of an inertial load linked to the hand. Specifically, typical participants perceived a hand as moving slower when it was pulling a toy car (linked to the car with a string) than when it was followed by the car (no string) (Takamuku et al., unpublished). As previously described, the effect can be explained based on the sequence of the inverse and the forward computations. This means that when the size of the effect differed between the two groups, both the forward and/or inverse computation could be abnormal in autism. However, we confirmed the effect was present with the same magnitude in both typical and ASC participants, indicating that both groups made similar use of the forward and inverse dynamics computation in their perception of visual motion. Considering the general difficulties in observing the internal computation, one may argue that either of the observed effects could be independent of the inverse computation. However, the combination of the two different implicit measures examined in this study strongly indicates that autistic adults correctly perform the inverse computation, at least, when estimating dynamic forces from the visual motion of objects.

Our results contrast with previous studies which have examined motor control, motor learning, and the processing of biological motion in autism. All these domains have been reported as abnormal in autism [Glazebrook et al., 2009; Koldewyn et al., 2010; Marko

et al., 2015] and all can be linked to the inverse computation. For example, earlier studies have reported impairments in biological motion detection [Blake et al., 2003; Koldewyn et al., 2010], reduced sensitivity to naturalness of hand motion [Cook, Saygin, Swain, & Blakemore, 2009], and deficits in perceiving dynamic facial expressions [Tardif et al., 2007; Uono et al., 2014; Shah et al., 2016]. However, there are also reports of normal motor control and learning [Gidley-Larson et al., 2008], and normal perception of biological motion [Jones et al. 2011; Cusack et al., 2015] in autism. Thus, our results add to these varied findings.

It is therefore important to consider why the field has found such mixed results. One possibility is the sample of participants used in different studies—autism is a heterogeneous developmental condition, and some papers have tested children while others test adults; other developmental disorders may also be comorbid with autism including dyspraxia. For example, studies of force field adaptation which showed less extrinsic representation of forces [Haswell et al., 2009] and lower sensitivity to visual perturbations [Marko et al., 2015] have tested children aged around 10 years (8–14 years). In our study, the sample comprised 27 autistic adults aged from 19 to 52 years. Recent meta-analyses have suggested a high degree of comorbidity of autism with dyspraxia [Miyahara, 2013] but dyspraxia cannot be seen as a core feature of autism given that many autistic individuals perform within the normal range on motor tasks [Emck, Bosscher, Beek, & Doreleijers, 2009]. The autism sample in our study self-reported lower motor skills on average compared to a neurotypical sample, yet there was a wide range of motor abilities in our autism sample with a many scoring within or above the neurotypical range (see Fig. 1). In the present sample, we found no correlation between the self-reported measures of motor skills and the measures of inverse dynamics we tested. Thus, the motor skills in our autism sample reflected the diversity of motor skill performance reported in autistic populations in previous studies [Gowen & Hamilton, 2013; Emck et al., 2009]. Although, the removal of the three participants with a comorbid dyspraxia diagnosis did not alter the results in the present study, the field may benefit from studying different subgroups of autistic individuals based on their motor skill performance.

A second possibility is the heterogeneity of tasks used to assess motor skill and motion perception. Different tasks and stimuli are used across different labs, and each task taps into many different computational mechanisms which makes it hard to pin down the locus of a difficulty [Gowen & Hamilton, 2013]. For example, force-field adaptation studies provide some of the clearest evidence for differences in motor learning [Haswell et al., 2009; Marko et al., 2015] but this task involves

both the inverse dynamics computation and the integration of visual and somatosensory signals while our study mostly involved only visual signals. Thus, lower sensitivity to visual signals in the previous studies of force field adaptation may simply reflect autistic people placing a larger weight on somatosensory feedback in their force estimation. Similarly, the tendency to represent force-fields in intrinsic rather than extrinsic coordinates can also be explained by a stronger reliance on somatosensory feedback. Thus, our studies are consistent with previous force-field studies if the latter revealed deficits in visual-proprioceptive integration rather than the inverse computation itself.

Concerning the neural mechanisms of the inverse computation, our results remain somewhat ambiguous. There is evidence linking the cerebellum to inverse computations [Shidara et al. 1993; Yamamoto et al., 2007] and to the perception of biological motion [Kilts, Egan, Gideon, Ely, & Hoffman, 2003; Sokolov, Gharabaghi, Tatagiba, & Pavlova, 2010; Sokolov et al. 2012; Sokolov, Erb, Grodd, & Pavlova, 2014]. There are also many studies linking cerebellar abnormalities to autism [Ritvo et al., 1986; Bailey et al., 1998; Kemper & Bauman, 1998; Whitney et al., 2008; Hashimoto et al., 1995; Murakami et al., 1989; D'Mello et al., 2015; Marko et al., 2015]. Nevertheless, our data imply that the cerebellar mechanisms which support the inverse dynamics computation are likely to be intact in autism. It is also possible that the participants with autism are achieving the same level of performance but using a different, compensatory mechanism. Given how fundamentally these basic visuomotor processes are linked to specific cerebellar cell types [Yamamoto et al., 2007], we think this is unlikely but future neuroimaging studies are required to confirm this.

While we used illusions to examine the ability of the inverse computation, an alternative approach to examine this ability would be to explicitly ask the participants about their sense of visually implied forces or the amount of effort an agent is putting into an action. For example, Baron-Cohen, Wheelwright, Spong, Scahill, and Lawson [2001] had children with Asperger Syndrome solve several physics problems and found that their understanding of physics was better than that of controls. However, it is unclear whether the participants relied on an internal computation of inverse dynamics or simply answered based on their physics reasoning. Such an argument, however, can be avoided in our case since we examined unavoidable distortions in our sensory perception which result from implicit processes of inverse computation. However, it should be noted that our purely behavioral study does not allow us to fully deny the possibility that the observed behaviors in ASC involved neural processes which differs from those of the neurotypical participants.

To summarize, our study rigorously tested the ability to use an inverse dynamics computation in autism by examining two distortions of sensory perception. The sensory distortions observed in the neurotypicals were present with comparable magnitude in the autistic group. This implies that the neural circuits for the inverse computation based on object motion signals are preserved, at least in the majority of the autistic adults. While earlier studies have suggested less use of visual feedback in motor learning [Marko et al., 2015] and abnormal internal models for motor control [Haswell et al., 2009], deficits in the extraction of force information from observed motion do not seem to account for these differences. Future studies could test how the use of inverse dynamics for visual perception is related to motor skills in participants with and without autism, and how these abilities relate to cerebellar structure and function.

### Acknowledgments

This work was supported by the UCL-NTT collaboration project. We thank Patrick Haggard for his assistance on running the project, Sam Gilbert for his assistance on testing the velocity perception task, and Kazushi Maruya for his comment on the design of the supplementary experiments. The experiments used Cogent Graphics developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience. AH and PF are supported by ERC grant INTERACT 313398.

### Conflict of Interest

The authors declare no conflicts of interest.

### References

- Aitkin, C.D., Santos, E.M., & Kowler, E. (2013). Anticipatory smooth eye movements in autism spectrum disorder. *PloS One*, 8, e83230.
- Anzulewicz, A., Sobota, K., & Delafield-Butt, J. (2016). Toward the autism motor signature. *Scientific Reports*, 6.
- Badler, J., Lefèvre, P., & Missal, M. (2010). Causality attribution biases oculomotor responses. *The Journal of Neuroscience*, 30, 10517–10525.
- Bailey, A., Luthert, P., Dean, A., Harding, B., Janota, I., Montgomery, M., ... Lantos, P. (1998). A clinicopathological study of autism. *Brain*, 121, 889–905.
- Baron-Cohen, S., Wheelwright, S., Spong, A., Scahill, V., & Lawson, J. (2001). Are intuitive physics and intuitive psychology independent? A test with children with Asperger Syndrome. *Journal of Developmental and Learning Disorders*, 5, 47–78.
- Bastiaansen, J.A., Meffert, H., Hein, S., Huizinga, P., Ketelaars, C., Pijnenborg, M., ... de Bildt, A. (2011). Diagnosing autism spectrum disorders in adults: the use of Autism

- Diagnostic Observation Schedule (ADOS) module 4. *Journal of Autism and Developmental Disorders*, 41, 1256–1266.
- Becker, W., & Fuchs, A.F. (1985). Prediction in the oculomotor system: Smooth pursuit during transient disappearance of a visual target. *Experimental Brain Research*, 57, 562–575.
- 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, 151–157.
- Blakemore, S.J., Wolpert, D.M., & Frith, C.D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, 1, 635–640.
- Blakemore, S.-J., Tavassoli, T., Calò, S., Thomas, R.M., Catmur, C., Frith, U., & Haggard, P. (2006). Tactile sensitivity in Asperger syndrome. *Brain and Cognition*, 61, 5–13.
- Brown, L.E., Wilson, E.T., Goodale, M.A., & Gribble, P.L. (2007). Motor force field learning influences visual processing of target motion. *The Journal of Neuroscience*, 27, 9975–9983.
- Brunner, E., & Munzel, U. (2000). The Nonparametric Behrens-Fisher Problem: Asymptotic Theory and a small-sample approximation. *Biometrical Journal*, 42, 17–25.
- Christensen, A., Ilg, W., & Giese, M.A. (2011). Spatiotemporal tuning of the facilitation of biological motion perception by concurrent motor execution. *The Journal of Neuroscience*, 31, 3493–3499.
- Conditt, M.A., Gandolfo, F., & Mussa-Ivaldi, F.A. (1997). The motor system does not learn the dynamics of the arm by rote memorization of past experience. *Journal of Neurophysiology*, 78, 554–560.
- Cook, J., Blakemore, S.-J., & Press, C. (2013). Atypical basic movement kinematics in autism spectrum conditions. *Brain*, 136, 2816–2824.
- Cook, J., Saygin, A.P., Swain, R., & Blakemore, S.-J. (2009). Reduced sensitivity to minimum-jerk biological motion in autism spectrum conditions. *Neuropsychologia*, 47, 3275–3278.
- Cook, J., Swapp, D., Pan, X., Bianchi-Berthouze, N., & Blakemore, S.-J. (2014). Atypical interference effect of action observation in autism spectrum conditions. *Psychological Medicine*, 44, 731–740.
- Cusack, J.P., Williams, J.H.G., & Neri, P. (2015). Action perception is intact in autism spectrum disorder. *The Journal of Neuroscience*, 35, 1849–1857.
- David, F.J., Baranek, G.T., Giuliani, C.A., Mercer, V.S., Poe, M.D., & Thorpe, D.E. (2009). A pilot study: Coordination of precision grip in children and adolescents with high functioning autism. *Pediatric Physical Therapy*, 21, 205–211.
- D’Mello, A.M., Crocetti, D., Mostofsky, S.H., & Stoodley, C.J. (2015). Cerebellar gray matter and lobular volumes correlate with core autism symptoms. *NeuroImage. Clinical*, 7, 631–639.
- Ego, C., Bonhomme, L., Orban de Xivry, J.-J., Da Fonseca, D., Lefèvre, P., Masson, G.S., & Deruelle, C. (2016). Behavioral characterization of prediction and internal models in adolescents with autistic spectrum disorders. *Neuropsychologia*, 91, 335–345.
- Emck, C., Bosscher, R., Beek, P., & Doreleijers, T. (2009). Gross motor performance and self-perceived motor competence in children with emotional, behavioural, and pervasive developmental disorders: A review. *Developmental Medicine and Child Neurology*, 51, 501–517.
- Flanagan, J.R., & Wing, A.M. (1997). The role of internal models in motion planning and control: Evidence from grip force adjustments during movements of hand-held loads. *The Journal of Neuroscience*, 17, 1519–1528.
- Foss-Feig, J.H., Tadin, D., Schauder, K.B., & Cascio, C.J. (2013). A substantial and unexpected enhancement of motion perception in autism. *The Journal of Neuroscience*, 33, 8243–8249.
- Fuentes, C.T., Mostofsky, S.H., & Bastian, A.J. (2011). No proprioceptive deficits in autism despite movement-related sensory and execution impairments. *Journal of Autism and Developmental Disorders*, 41, 1352–1361.
- Gidley-Larson, J.C., Bastian, A.J., Donchin, O., Shadmehr, R., & Mostofsky, S.H. (2008). Acquisition of internal models of motor tasks in children with autism. *Brain*, 131, 2894–2903.
- Glazebrook, C., Gonzalez, D., Hansen, S., & Elliott, D. (2009). The role of vision for online control of manual aiming movements in persons with autism spectrum disorders. *Autism*, 13, 411–433.
- Gowen, E. (2012). Imitation in autism: why action kinematics matter. *Frontiers in Integrative Neuroscience*, 6, 117.
- Gowen, E., & Hamilton, A. (2013). Motor abilities in autism: A review using a computational context. *Journal of Autism and Developmental Disorders*, 43, 323–344.
- Gowen, E., & Miall, R.C. (2005). Behavioural aspects of cerebellar function in adults with Asperger syndrome. *Cerebellum*, 4, 279–289.
- Gowen, E., Stanley, J., & Miall, R.C. (2008). Movement interference in autism-spectrum disorder. *Neuropsychologia*, 46, 1060–1068.
- Green, D., Charman, T., Pickles, A., Chandler, S., Loucas, T., Simonoff, E., & Baird, G. (2009). Impairment in movement skills of children with autistic spectrum disorders. *Developmental Medicine and Child Neurology*, 51, 311–316.
- Hamilton, A.F., de, C., Joyce, D.W., Flanagan, J.R., Frith, C.D., & Wolpert, D.M. (2007). Kinematic cues in perceptual weight judgement and their origins in box lifting. *Psychological Research*, 71, 13–21.
- Hashimoto, T., Tayama, M., Murakawa, K., Yoshimoto, T., Miyazaki, M., Harada, M., & Kuroda, Y. (1995). Development of the brainstem and cerebellum in autistic patients. *Journal of Autism and Developmental Disorders*, 25, 1–18.
- Haswell, C.C., Izawa, J., Dowell, L.R., Mostofsky, S.H., & Shadmehr, R. (2009). Representation of internal models of action in the autistic brain. *Nature Neuroscience*, 12, 970–972.
- Honda, T., Hagura, N., & Imamizu, H. (2013). Imposed visual feedback delay of an action changes mass perception based on the sensory prediction error. *Frontiers in Consciousness Research*, 4, 760.
- Hu, B., & Knill, D.C. (2010). Kinesthetic information disambiguates visual motion signals. *Current Biology*, 20, R436–R437.
- Jansiewicz, E.M., Goldberg, M.C., Newschaffer, C.J., Denckla, M.B., Landa, R., & Mostofsky, S.H. (2006). Motor signs distinguish children with high functioning autism and Asperger’s syndrome from controls. *Journal of Autism and Developmental Disorders*, 36, 613–621.

- Johnson, B.P., Rinehart, N.J., White, O., Millist, L., & Fielding, J. (2013). Saccade adaptation in autism and Asperger's disorder. *Neuroscience*, 243, 76–87.
- Jones, C.R.G., Swettenham, J., Charman, T., Marsden, A.J.S., Tregay, J., Baird, G., ... Happé, F. (2011). No evidence for a fundamental visual motion processing deficit in adolescents with autism spectrum disorders. *Autism Research*, 4, 347–357.
- Jordan, M.I., & Rumelhart, D.E. (1992). Forward models: Supervised learning with a distal teacher. *Cognitive Science*, 16, 307–354.
- Kawato, M., & Gomi, H. (1992). A computational model of four regions of the cerebellum based on feedback-error learning. *Biological Cybernetics*, 68, 95–103.
- Kemper, T.L., & Bauman, M. (1998). Neuropathology of infantile autism. *Journal of Neuropathology and Experimental Neurology*, 57, 645–652.
- Kilts, C.D., Egan, G., Gideon, D.A., Ely, T.D., & Hoffman, J.M. (2003). Dissociable neural pathways are involved in the recognition of emotion in static and dynamic facial expressions. *NeuroImage*, 18, 156–168.
- Koldewyn, K., Whitney, D., & Rivera, S.M. (2010). The psychophysics of visual motion and global form processing in autism. *Brain*, 133, 599–610.
- La Scaleia, B., Zago, M., Moscatelli, A., Lacquaniti, F., & Viviani, P. (2014). Implied dynamics biases the visual perception of velocity. *PloS One*, 9, e93020.
- Manjiviona, J., & Prior, M. (1995). Comparison of Asperger syndrome and high-functioning autistic children on a Test of Motor Impairment. *Journal of Autism and Developmental Disorders*, 25, 23–39.
- Manning, C., Tibber, M.S., Charman, T., Dakin, S.C., & Pellicano, E. (2015). Enhanced integration of motion information in children with autism. *The Journal of Neuroscience*, 35, 6979–6986.
- Marko, M.K., Crocetti, D., Hulst, T., Donchin, O., Shadmehr, R., & Mostofsky, S.H. (2015). Behavioural and neural basis of anomalous motor learning in children with autism. *Brain*, 138, 784–797.
- Mattar, A.A.G., & Gribble, P.L. (2005). Motor learning by observing. *Neuron*, 46, 153–160.
- Miall, R.C., Christensen, L.O.D., Cain, O., & Stanley, J. (2007). Disruption of state estimation in the human lateral cerebellum. *PLoS Biology*, 5, e316.
- Michotte, A. (1963). *The perception of causality* (Vol. xxii). Oxford, England: Basic Books.
- Miyahara, M. (2013). Meta review of systematic and meta analytic reviews on movement differences, effect of movement based interventions, and the underlying neural mechanisms in autism spectrum disorder. *Frontiers in Integrative Neuroscience*, 7, 16.
- Mosconi, M.W., Luna, B., Kay-Stacey, M., Nowinski, C.V., Rubin, L.H., Scudder, C., ... Sweeney, J.A. (2013). Saccade adaptation abnormalities implicate dysfunction of cerebellar-dependent learning mechanisms in Autism Spectrum Disorders (ASD). *PloS One*, 8, e63709.
- Mosconi, M.W., Mohanty, S., Greene, R.K., Cook, E.H., Vaillancourt, D.E., & Sweeney, J.A. (2015). Feedforward and feedback motor control abnormalities implicate cerebellar dysfunctions in autism spectrum disorder. *The Journal of Neuroscience*, 35, 2015–2025.
- Murakami, J.W., Courchesne, E., Press, G.A., Yeung-Courchesne, R., & Hesselink, J.R. (1989). Reduced cerebellar hemisphere size and its relationship to vermal hypoplasia in autism. *Archives of Neurology*, 46, 689–694.
- Nanayakkara, T., & Shadmehr, R. (2003). Saccade adaptation in response to altered arm dynamics. *Journal of Neurophysiology*, 90, 4016–4021.
- Parovel, G., & Casco, C. (2006). The psychophysical law of speed estimation in Michotte's causal events. *Vision Research*, 46, 4134–4142.
- Reichelt, A.F., Ash, A.M., Baugh, L.A., Johansson, R.S., & Flanagan, J.R. (2013). Adaptation of lift forces in object manipulation through action observation. *Experimental Brain Research*, 228, 221–234.
- Ritvo, E.R., Freeman, B.J., Scheibel, A.B., Duong, T., Robinson, H., Guthrie, D., & Ritvo, A. (1986). Lower Purkinje cell counts in the cerebella of four autistic subjects: Initial findings of the UCLA-NSAC Autopsy Research Report. *The American Journal of Psychiatry*, 143, 862–866.
- Runeson, S. (1974). Constant velocity—not perceived as such. *Psychological Research*, 37, 3–23.
- Runeson, S., & Frykholm, G. (1981). Visual perception of lifted weight. *Journal of Experimental Psychology. Human Perception and Performance*, 7, 733–740.
- Sarlegna, F.R., Baud-Bovy, G., & Danion, F. (2010). Delayed visual feedback affects both manual tracking and grip force control when transporting a handheld object. *Journal of Neurophysiology*, 104, 641–653.
- Schmitt, L.M., Cook, E.H., Sweeney, J.A., & Mosconi, M.W. (2014). Saccadic eye movement abnormalities in autism spectrum disorder indicate dysfunctions in cerebellum and brainstem. *Molecular Autism*, 5, 47.
- Schmitz, C., Martineau, J., Barthélémy, C., & Assaiante, C. (2003). Motor control and children with autism: Deficit of anticipatory function?. *Neuroscience Letters*, 348, 17–20.
- Shadmehr, R., & Mussa-Ivaldi, F.A. (1994). Adaptive representation of dynamics during learning of a motor task. *The Journal of Neuroscience*, 14, 3208–3224.
- Shah, P., Bird, G., & Cook, R. (2016). Face processing in autism: Reduced integration of cross-feature dynamics. *Cortex*, 75, 113–119.
- Shidara, M., Kawano, K., Gomi, H., & Kawato, M. (1993). Inverse-dynamics model eye movement control by Purkinje cells in the cerebellum. *Nature*, 365, 50–52.
- Sokolov, A.A., Erb, M., Gharabaghi, A., Grodd, W., Tatagiba, M.S., & Pavlova, M.A. (2012). Biological motion processing: The left cerebellum communicates with the right superior temporal sulcus. *NeuroImage*, 59, 2824–2830.
- Sokolov, A.A., Erb, M., Grodd, W., & Pavlova, M.A. (2014). Structural loop between the cerebellum and the superior temporal sulcus: Evidence from diffusion tensor imaging. *Cerebral Cortex*, 24, 626–632.
- Sokolov, A.A., Gharabaghi, A., Tatagiba, M.S., & Pavlova, M. (2010). Cerebellar engagement in an action observation network. *Cerebral Cortex*, 20, 486–491.
- Sotiropoulos, G., Seitz, A.R., & Seriès, P. (2011). Changing expectations about speed alters perceived motion direction. *Current Biology*, 21, R883–R884.
- Stocker, A.A., & Simoncelli, E.P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience*, 9, 578–585.

- Takamuku, S., & Gomi, H. (2015). What you feel is what you see: Inverse dynamics estimation underlies the resistive sensation of a delayed cursor. *Proceedings. Biological Sciences/the Royal Society*, 282, 20150864.
- Takarae, Y., Luna, B., Minshew, N.J., & Sweeney, J.A. (2008). Patterns of visual sensory and sensorimotor abnormalities in autism vary in relation to history of early language delay. *Journal of the International Neuropsychological Society*, 14, 980–989.
- Takarae, Y., Minshew, N.J., Luna, B., Krisky, C.M., & Sweeney, J.A. (2004). Pursuit eye movement deficits in autism. *Brain*, 127, 2584–2594.
- Takarae, Y., Minshew, N.J., Luna, B., & Sweeney, J.A. (2007). Atypical involvement of frontostriatal systems during sensorimotor control in autism. *Psychiatry Research*, 156, 117–127.
- Takarae, Y., Minshew, N., Luna, B., & Sweeney, J. (2004). Oculomotor abnormalities parallel cerebellar histopathology in autism. *Journal of Neurology, Neurosurgery, and Psychiatry*, 75, 1359–1361.
- Tardif, C., Lainé, F., Rodriguez, M., & Gepner, B. (2007). Slowing down presentation of facial movements and vocal sounds enhances facial expression recognition and induces facial-vocal imitation in children with autism. *Journal of Autism and Developmental Disorders*, 37, 1469–1484.
- Teitelbaum, P., Teitelbaum, O., Nye, J., Fryman, J., & Maurer, R.G. (1998). Movement analysis in infancy may be useful for early diagnosis of autism. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 13982–13987.
- Théoret, H., Halligan, E., Kobayashi, M., Fregni, F., Tager-Flusberg, H., & Pascual-Leone, A. (2005). Impaired motor facilitation during action observation in individuals with autism spectrum disorder. *Current Biology*, 15, R84–R85.
- Uono, S., Sato, W., & Toichi, M. (2014). Reduced representational momentum for subtle dynamic facial expressions in individuals with autism spectrum disorders. *Research in Autism Spectrum Disorders*, 8, 1090–1099.
- Weiss, Y., Simoncelli, E.P., & Adelson, E.H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, 5, 598–604.
- White, P.A. (2012). The experience of force: The role of haptic experience of forces in visual perception of object motion and interactions, mental simulation, and motion-related judgments. *Psychological Bulletin*, 138, 589–615.
- Whitney, E.R., Kemper, T.L., Bauman, M.L., Rosene, D.L., & Blatt, G.J. (2008). Cerebellar Purkinje cells are reduced in a subpopulation of autistic brains: A stereological experiment using calbindin-D28k. *Cerebellum*, 7, 406–416.
- Wilson, B.N., Kaplan, B.J., Crawford, S.G., & Roberts, G. (2007). The developmental coordination disorder questionnaire 2007 (DCDQ'07). *Administrative Manual for the DCDQ107 with Psychometric Properties*.
- Wolpert, D.M., Ghahramani, Z., & Jordan, M.I. (1995). An internal model for sensorimotor integration. *Science*, 269, 1880–1882.
- Yamamoto, K., Kawato, M., Kotosaka, S., & Kitazawa, S. (2007). Encoding of movement dynamics by Purkinje cell simple spike activity during fast arm movements under resistive and assistive force fields. *Journal of Neurophysiology*, 97, 1588–1599.

## Supporting Information

Additional Supporting Information may be found in the online version of this article.