



Seeing motion of controlled object improves grip timing in adults with autism spectrum condition: evidence for use of inverse dynamics in motor control

Shinya Takamuku¹ · Haruhisa Ohta² · Chieko Kanai^{2,3} · Antonia F. de C. Hamilton⁴ · Hiroaki Gomi¹

Received: 15 September 2020 / Accepted: 18 January 2021

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Abstract

Previous studies (Haswell et al. in *Nat Neurosci* 12:970–972, 2009; Marko et al. in *Brain J Neurol* 138:784–797, 2015) reported that people with autism rely less on vision for learning to reach in a force field. This suggested a possibility that they have difficulties in extracting force information from visual motion signals, a process called inverse dynamics computation. Our recent study (Takamuku et al. in *J Int Soc Autism Res* 11:1062–1075, 2018) examined the ability of inverse computation with two perceptual tasks and found similar performances in typical and autistic adults. However, this tested the computation only in the context of sensory perception while it was possible that the suspected disability is specific to the motor domain. Here, in order to address the concern, we tested the use of inverse dynamics computation in the context of motor control by measuring changes in grip timing caused by seeing/not seeing a controlled object. The motion of the object was informative of its inertial force and typical participants improved their grip timing based on the visual feedback. Our interest was on whether the autism participants show the same improvement. While some autism participants showed atypical hand slowing when seeing the controlled object, we found no evidence of abnormalities in the inverse computation in our grip timing task or in a replication of the perceptual task. This suggests that the ability of inverse dynamics computation is preserved not only for sensory perception but also for motor control in adults with autism.

Keywords Autism · Internal models · Inverse dynamics · Grip force control · Visuomotor control

Introduction

Motor difficulties are common in people with autism spectrum condition (ASC) with up to 89% co-morbidity of autism and motor problems (Green et al. 2009; Fournier et al. 2010; Bhat et al. 2011). While standard test batteries

provide rough pictures of the difficulties, understanding which computational processes of motor control (Gowen and Hamilton 2013) are atypical would be preferable for designing better training methods and accessible tools.

Performing a voluntary action involves multiple processes such as planning a motor action, executing the action, and processing the sensory feedback to adjust current and future actions. While abnormality in people with ASC are reported for all of these processes (Gowen and Hamilton 2013), our study focused on the ability to extract relevant information from sensory feedbacks to adjust our motor action.

In this regard, several studies have suggested abnormal use of visual feedback in motor control and motor learning in people with autism. Glazebrook and her colleagues examined durations of reaching movements made with and without vision (Glazebrook et al. 2009). They found that adults with autism took significantly longer to complete the movement when vision was provided while the increase was much smaller in the typicals. Gidley-Larson et al. (2008) examined the ability of motor learning in children with

Communicated by Melvyn A. Goodale.

✉ Shinya Takamuku
shinya.takamuku.ka@hco.ntt.co.jp

¹ NTT Communication Science Laboratories, Nippon Telegraph and Telephone Corporation, Atsugi, Kanagawa, Japan

² Medical Institute of Developmental Disabilities Research, Showa University, Setagaya-ku, Tokyo, Japan

³ Department of Child Development and Education, Wayo Women's University, Ichikawa, Chiba, Japan

⁴ Institute of Cognitive Neuroscience, University College London, London, UK

autism though a variety of adaptation tasks; prism adaptation, visuomotor rotation, and force-field adaptation. They reported that the rate of adaptation did not differ with those of the typicals in either of the tasks. However, several studies which examined these adaptation in more depth suggested atypical uses of visual feedbacks. For example, Masterton and Biederman (1983) reported that children with autism generalized prism adaptation to the non-adapted hand even when visual feedback was provided throughout the reaching period. In typicals, such generalization is observed only when online visual feedback is prohibited during the reaching movements.

Series of studies which observed the abnormal use of visual feedback in force-field adaptation were of particular interest to our study. In force-field adaptation, participants learn to make a straight reaching movement in a force-field which pulls the hand to the side. Both visual and proprioceptive signals can contribute to this learning. Marko and his colleague found that children with autism rely less on visual feedback compared to the typicals (Marko et al. 2015). This was consistent with an earlier finding (Haswell et al. 2009; Izawa et al. 2012) which showed that children with autism tend to represent the force-field in proprioceptive (intrinsic) rather than visual (extrinsic) coordinates. The latter finding was based on spatial pattern in generalizing the adaptation. The abnormality correlated with various measures of autism (Haswell et al. 2009) and was found to be specific to autism (not observed in children with ADHD; Izawa et al. 2012). Marko et al. showed in their study that the sensorimotor cerebellum was smaller in participants with autism and that the size of this cerebellar region correlated with the visual sensitivity in force-field adaptation (Marko et al. 2015). Considering evidence (Wolpert et al. 1998; Honda et al. 2018; Popa and Ebner 2018; Tanaka et al. 2020) that the cerebellum embeds internal models of our body and the world we interact with to optimize our motor behavior, Marko and colleagues suggested that atypical motor learning in autism may be related to the difference in such internal models.

What type of internal model could underlie the visual contribution to force-field adaptation? One candidate would be internal models for inverse dynamics computation (Kawato 1999). Inverse dynamics computation refers to the process of specifying force information that corresponds to a given motion information. The concept is often used to explain the process of motor planning, (Kawato and Gomi 1992; Shadmehr and Mussa-Ivaldi 1994; Ghasia et al. 2008; Honda et al. 2018); i.e., how we specify motor command signals (force information) that generates a desired body movement (motion information). Physiological evidence of the inverse computation came from recording of Purkinje cell activities in the cerebellum for eye and arm movements (Shidara et al. 1993; Kobayashi et al. 1998; Yamamoto et al. 2007; although see Ostry and

Feldman 2003; Pasalar et al. 2006) as well as premotor cells in the brainstem (Green et al. 2007; Ghasia et al. 2008).

Importantly, inverse dynamics computation can also be used for processing visual feedbacks; to extract force information from observed motions. For example, one can estimate how hard one have hit a golf ball from its resulting motion. Recently, the authors have suggested that such process underlies our ability to monitor our motor action. In one study (Takamuku and Gomi 2015), we found that the illusory kinetic sensation experienced while moving a delayed cursor correlates with its forward acceleration. This suggested that we estimate the inertial reaction force of objects we control from their visual motion using inverse dynamics. In another study (Takamuku and Gomi 2019) we supported this hypothesis by showing that temporal control of grip force improves when one sees the motion of the controlled object. Since grip force is adjusted to correlate with the expected load force (Flanagan and Wing 1997), the finding suggested that the visual feedback contributed to the force estimation. While several theories suggest that sensory feedbacks are processed in accord to our prediction (Frith et al. 2000; Carota et al. 2010) or to spatial frames defined by referent signals (Feldman 2016), our studies showed that neither the kinetic sensation nor the improvement in grip force control can be explained based on such error-based framework.

In the context of force-field adaptation, studies suggest that the adaptation partly depends on building an extrinsic representation of the force field based on vision (Mattar and Gribble 2005; Brown et al. 2007; Williams and Gribble 2012). Estimating the force field from the motion of the controlled hand cursor can theoretically be interpreted as a form of vision-driven inverse dynamics computation. Considering reports of abnormal visual feedback processing, less use of visual feedback in the adaptation, and less generalization in visual coordinates, the authors hypothesized that people with autism may have difficulty in this inverse computation.

In a recent study, Takamuku et al. (2018) tested the use of inverse dynamics computation in adults with autism and age- and IQ- matched controls by examining the illusory kinetic sensation experienced while moving a delayed cursor and a bias in velocity perception linked to visually implied inertia, both suggested to depend on the inverse computation of force information from visual motion signals. In both tasks, typical and autistic participants showed similar evidence for the use of inverse dynamics computations.

One concern, however, was that the study only tested the ability of the inverse computation in the context of visual perception. Many studies have suggested possibilities that visual processing for motor control differs from those for sensory perception (Goodale and Milner 1992; Westwood and Goodale 2011). Interestingly, some of these studies

suggested that processing of visual motion (Bridgeman et al. 1981; Goodale et al. 1986; Gomi et al. 2006) as well as those related to force-estimation (Flanagan and Beltzner 2000; Platkiewicz and Hayward 2014) differ depending on whether the goal is a motor action or a perception. Meanwhile, series of studies on autism suggested abnormality in the dorsal pathway of the visual system (Gepner et al. 1995; Spencer et al. 2000; McCleery et al. 2007; Sutherland and Crewther 2010; Foss-Feig et al. 2013; Takarae et al. 2014). These findings suggested a possibility that vision-based inverse computation for motor control differs from those for sensory perception and that people with autism have a deficit specific to the motor domain.

Here, in order to test this hypothesis, we recruited a new sample of adults with ASC and their age- and IQ-matched controls, and asked these participants to perform both a perception test of the inverse computation and a motor action test of the inverse computation. The perception test replicated the earlier study of biases in velocity perception (Takamuku et al. 2018). This tested whether our perception of object velocity depends on visually implied inertial force disturbing the object motion. The motor action test assesses whether participants improve their grip force control when they can see an object as they move that object back and forth (comparison to condition without visual feedback); this forementioned effect is also suggested to depend on the inverse computation (Takamuku and Gomi 2019; Sarlegna et al. 2010). If people with autism have a deficit in inverse computation specific to motor control, they would show the expected effect only in the perception task. On the other hand, if they have intact ability in both inverse computations, they should show the expected effects in both tasks. Our study thus aimed to dissociate these possibilities.

Method

Participants

Twenty-five adults with ASC and ten neuro-typical (NT) adults participated in the study (Table 1). The power of detecting the expected effects in the NT group was above 0.8 for both tasks (power analysis based on previous data; Takamuku et al. 2018; Takamuku and Gomi 2019). More participants were recruited for autism group considering their diversity. Some autism participants were excluded from analysis due to poor performance in each experiment, but the two groups were always matched for age, gender and IQ. All participants were right-handed. IQ of ASC participants were measured using the Japanese version of the Wechsler Adult Intelligence Scale (WAIS-III). IQ of typical participants were measured using a short form of the Wechsler Adult Intelligence Scale III (Dairoku 2011), the detail of which described in section S1 in the Supplementary Information. None of the typical participants showed a significant level of autistic symptomatology (score of 33 or more) as measured by the Japanese version of the Autism-Spectrum Quotient (AQ) test (Wakabayashi et al. 2007).

The ASC participants were recruited from the patient unit of Karasuyama Hospital, Tokyo, Japan. The diagnosis of ASC was based on the consensus of two experienced psychiatrists according to the criteria of the Diagnostic and Statistical Manual of Mental Disorders (DSM-5). One participant had a diagnosis of Attention Deficit Disorder (ADD). The Autism Diagnostic Observation Schedule (ADOS-2) Module 4 scores were measured by a research licensed clinical psychologist (C.K.). Thirteen participants met the ADOS-2 classification for autism, 10 for autism spectrum, and two 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

Table 1 Comparison of the typical and the autistic (ASC) groups

	NT (<i>N</i> = 10)		ASD (<i>N</i> = 25)		<i>t</i> test
	Mean (SD)	Range	Mean (SD)	Range	<i>p</i> value
Age (years)	29.6 (9.4)	20–43	29.3 (6.1)	20–45	0.93
Gender	3F; 7 M	–	3F; 22 M	–	–
Handedness	10R	–	25R	–	–
Fullscale IQ	102.6 (9.4)	82–120	103.1 (11.8)	82–135	0.90
Verbal IQ	–	–	108.8 (13.2)	82–140	–
Performance IQ	–	–	95.1 (13.1)	71–123	–
AQ score	18.2 (5.2)	7–25	34.6 (6.5)	23–45	0.00***
ADOS: total	–	–	11.6 (5.8)	6–31	–
ADOS: communication	–	–	4.5 (3.3)	1–15	–
ADOS: social interaction	–	–	7.1 (2.8)	4–16	–

* $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$

on either the Communication subscale or the Reciprocal Social Interaction subscale, and all had a clear diagnostic history. Since the sensitivity of ADOS in adults with high IQ is rather low (Bastiaansen et al. 2011), we did not exclude the participants based on the ADOS-2 criteria.

Design of perception experiment

The perception experiment tested the use of inverse computation for perception. Figure 1 illustrates the design of the experiment. Here, participants viewed a hand (Fig. 1a) moving from left to right and back repeatedly on a computer screen with their peripheral vision while fixating on a fixation point shown at the center of the screen. The screen was placed approximately 57 cm from their eyes. In one case, the hand was pulling a red car (pulling condition). This was indicated by a black string connecting the car to the hand.

In another case, the hand was followed by the same car (followed condition) without the string. In both conditions, the hand and the car followed a sinusoidal trajectory with a movement cycle of 1.2 s with the car having a phase lag of 90° (Fig. 1b) relative to the hand.

An earlier study showed that the hand pulling the car is perceived to be slower than the hand followed by the car (Takamuku et al. 2018). The effect was explained based on the theories that our motion percept is formed by Bayesian integration of expected and observed motions (Weiss et al. 2002; Stocker and Simoncelli 2006; Hu and Knill 2010), the expectation reflects internal models of dynamics shaped by sensorimotor experiences of forces (Brown et al. 2007; White 2012), and dynamic forces can be estimated from visual motion of controlled objects (Takamuku and Gomi 2015). Namely, in the pulling condition, the motion of the car implies its inertial force disturbing the hand motion

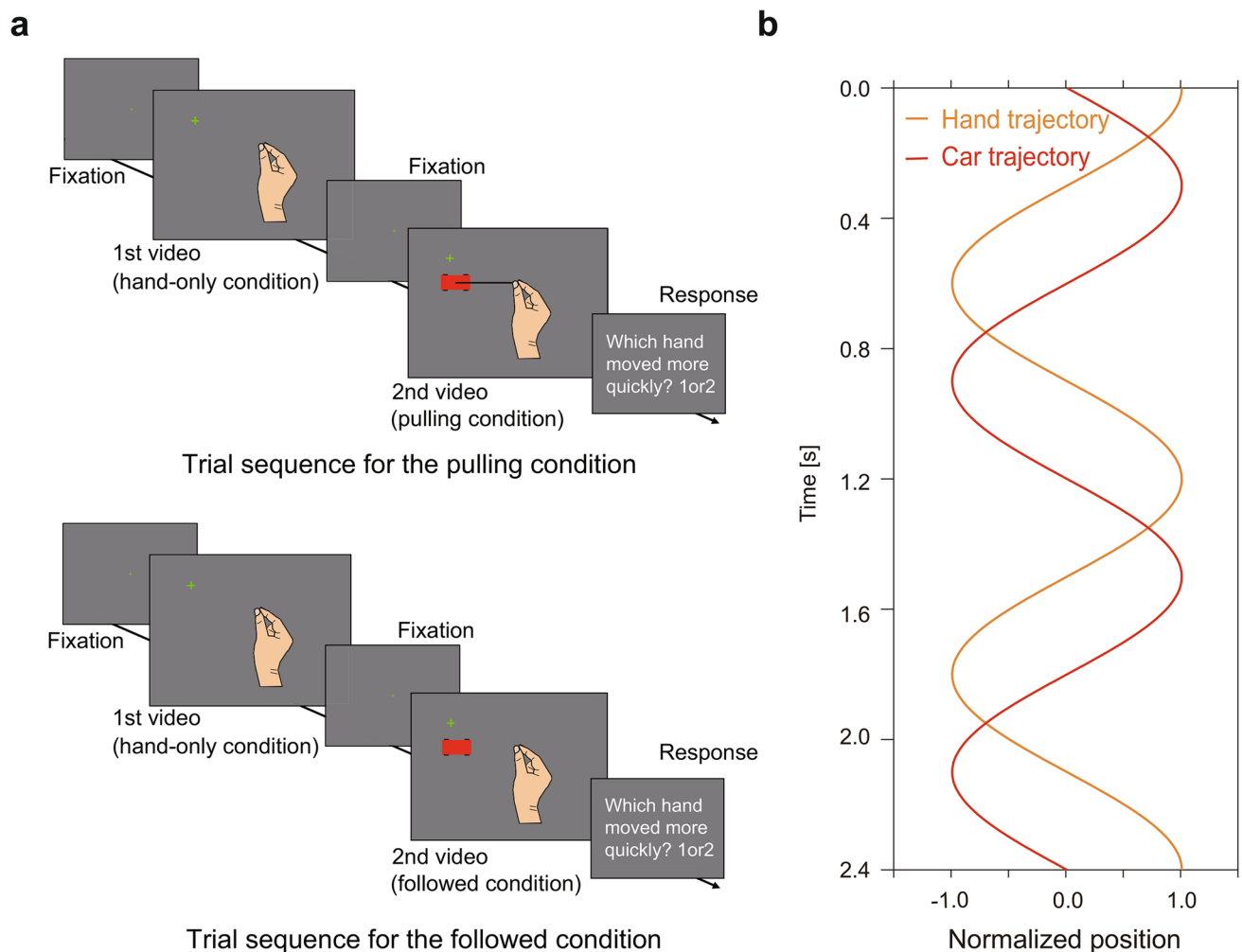


Fig. 1 Design of perception experiment. **a** Trial sequence for the pulling and followed conditions. Cropped images are shown for the stimuli used for the hand-only (control), followed, and pulling conditions

to increase visibility. **b** Trajectory of the hand and the car in the pulling and followed conditions

(inverse computation). This forms an expectation that the hand would decelerate and integrating the expectation makes the hand appear slow. The theory predicts that the effect would depend on the motion of the car. This was tested in experiments with typical adults (supplementary data of Takamuku et al. 2018). The magnitude of the effect did vary depending on the motion (phase delay) of the car and disappeared under stroboscopic condition. Importantly, the effect cannot be explained by any local motion interactions, since motion signals are identical between the two conditions. Furthermore, while attentional tracking could influence motion perception (Corbetta et al. 1991; Cavanagh 1992; Nakayama and Motoyoshi 2017), there were no evidence for difference in levels of attention between the two conditions (no difference in JND).

To measure the effect, we asked participants to judge how fast the hand was moving in each condition. The perceived velocities of the hand in these conditions were measured by comparing its velocity against the hand moving by itself (hand-only condition) at different velocities (movement cycle of 1.05, 1.12, 1.17, 1.2, 1.23, 1.28, or 1.35 s; method of constant stimuli) in separate blocks. Each comparison was made 16 times. A logistic psychometric function was fit to each data to obtain both the point of subjective equality (PSE) and the just-noticeable difference (JND) for each condition. Then the bias in velocity perception, linked to the inverse computation, was evaluated by examining whether the perceived velocity of the hand was significantly slower in the pulling condition than in the followed condition.

Two-factor-ANOVA with group as between-subject factor and stimuli condition (pulling or followed) as within-subject factor was applied to analyze the PSEs and the JNDs. Participants with JND larger than the tested range was excluded from both analysis due to low reliability of their measurements (exclusion criteria used in Takamuku et al. 2018). Two participants in the ASC group were excluded from analysis based on this criteria. Age, gender and IQ were still matched between the two groups after the exclusion (section S2 in Supplementary Information). Further details of the task can be found in (Takamuku et al. 2018).

Design of motor action experiment

The motor action experiment tested the use of inverse computation for motor control. Figure 2 illustrates the design of the motor experiment. Participants sat in front of a table and pinched a cube attached to an end of a robot (Phantom premium 1.5 A, Geomagic Inc.) placed below the table (bottom part of Fig. 2a). An LCD placed flat immediately over the table was used to provide visual cues (Fig. 2a). The participant's task was to repeatedly move the cube from side-to-side with specified movement amplitude and cycle. To help participants maintain the correct

movement amplitude, markers at the edge of the movement area changed from dark to light grey when they reached the end of the area. A periodic beep every 0.5 s was used to cue the rhythm of the movements. Throughout the task, participants were asked to fixate on a central cross on the LCD and each trial lasted 10 s.

A virtual object (mass) was attached to the cube with a damped spring (spring-mass-damper system; the middle part of Fig. 2a). The position of the object (y [m]) was updated at 1 [KHz] based on the measured position of the cube (x [m]) by applying the 4th-order Runge–Kutta method to the following equation of motion;

$$m\ddot{y} = d(\dot{x} - \dot{y}) + k(x - y) \quad (1)$$

M (kg), d (Ns/m), and k (N/m) represents the mass, damping factor, and stiffness of the spring, respectively. These values were set so that the object would follow the cube with a specific phase delay while the cube moved back-and-forth in the specified manner (Fig. 2b; see Takamuku and Gomi 2019 for detail). The inertial reaction force of the object ($F = m\ddot{y}$ [N]) was then applied to the cube by the Phantom robot. This implicitly required the participants to scale their grip force in correlation with the load force (the inertial force of the object) in order to prevent the cube from slipping out of their fingers and to avoid producing the grip force all the time. We also varied the stiffness (k) and the damping factor (d) of the virtual spring such that the object follows the hand either with a phase delay of approximately 80 and 100° (load force condition of either small or large delay; Fig. 2b). The load force condition changed across trials. This further required the participants to adjust the grip timing to match the load force timing of each condition.

Under such setup, grip force tends to precede the load force. However, importantly, an earlier study on typical adults showed that they decrease this temporal asynchrony when visual feedback of object position is provided (Takamuku and Gomi 2019). Since grip force is adjusted in prediction of the load force (Flanagan and Wing 1997) and the motion of the object is informative of the applied load force, the improvement in grip timing was interpreted as evidence that the participants gained a better estimate of the load force by extracting the force information from the motion of the object (inverse computation). The idea that inertial force of a controlled object is extracted from its motion is supported in our previous study on the sensation caused by delayed visual feedback (Takamuku and Gomi 2015). Furthermore, the idea that such force estimation process contributes to grip force adjustment is also supported by the study of Sarlegna et al. (2010).

Our interest was in whether the improvement in grip timing can also be observed in adults with ASC. In order to compare the effect between the two groups, we first

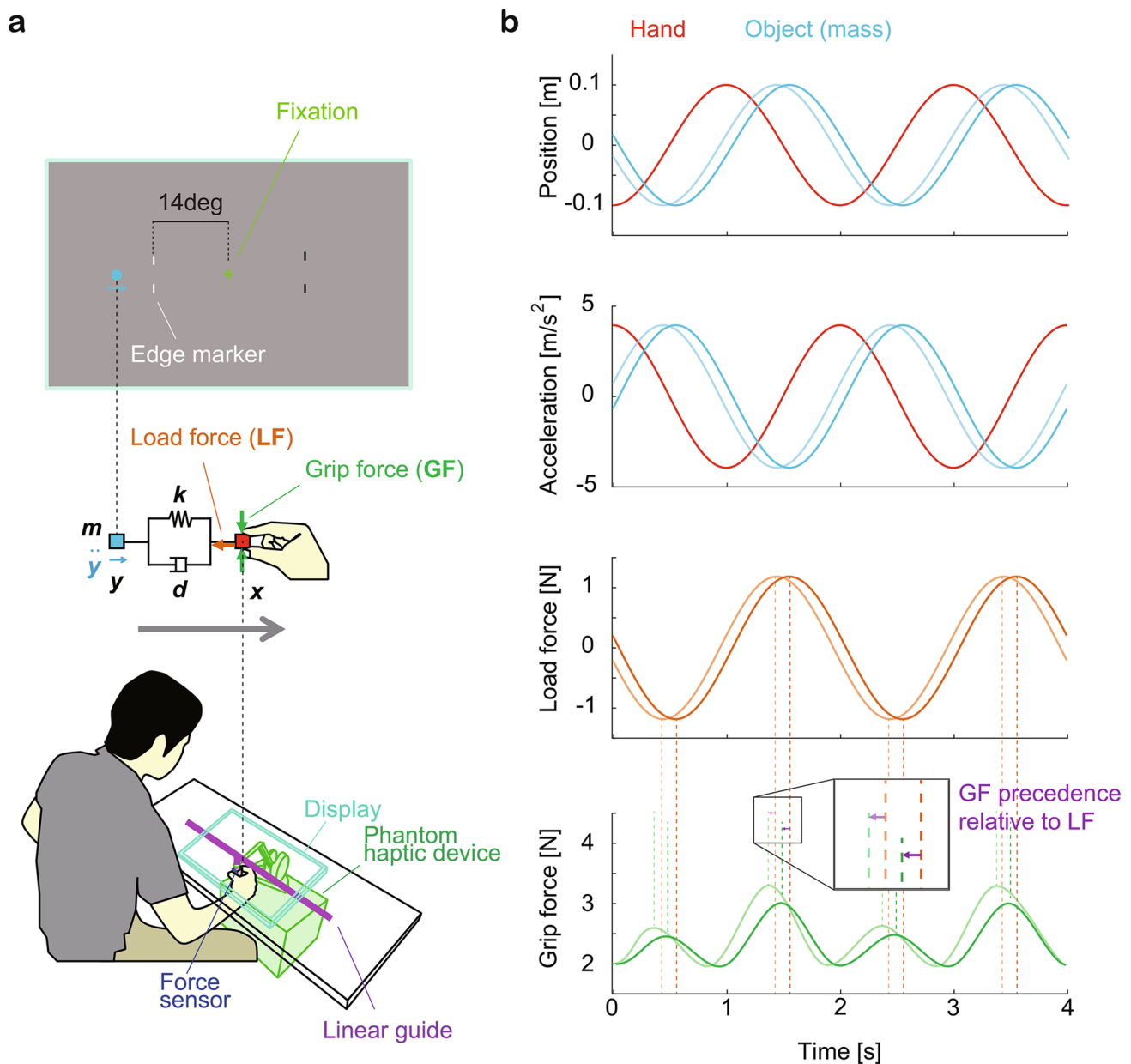


Fig. 2 Design of motor action experiment. **a** Top, middle and bottom parts show the image shown on the display, the virtual mechanical system controlled by the participant and the setup, respectively. **b** Illustration of the expected hand/object trajectories and the grip and

load force patterns (light color: small delay condition, dark color: large delay condition). Panel in the bottom indicates the grip force precedence relative to the load force measured in the study as the index of the inverse computation

examined how the visual feedback influenced the hand trajectory. This was because the load force pattern depended on the hand trajectory and any difference in the trajectory may influence the grip-load force coupling. The influence was assessed in terms of movement cycle since providing the visual feedback of object position tends to slow down the hand movement (Takamuku and Gomi 2019). Then, subgroup of autism participants whose hand movement cycle were within the typical range (< 2 SD) were defined for comparing the grip timing improvement with the typicals.

We quantified the grip timing in terms of the temporal asynchrony between grip force and load force on each trial, where low asynchrony scores indicate good performance. Participants performed the task with visual feedback of the object location and without visual feedback under two load-force timings, in a 2×2 factorial design. Each condition was tested 32 times and the conditions were randomized across trials. The temporal asynchrony between the grip and load forces was calculated by taking the cross-correlation between the two forces (see section S3 in Supplementary

Information). Since the grip force tended to precede the load force in all conditions, we hereafter refer to the temporal asynchrony as the grip force precedence relative to the load force.

Three-factor-ANOVA with group as between-subject factor and visual (with or without visual feedback) and load force (80 or 100° delay) conditions as within-subject factor was applied to analyze the measured behavioural indexes (hand movement features and grip-load asynchrony). Further detail on the experiment can be found in Takamuku and Gomi (2019).

Bayesian factor hypothesis testing

In order to enable further interpretation of null results, we applied Bayesian factor hypothesis testing (Keyes et al. 2020) to the between-group comparison of the measures of the inverse computation obtained in the two experiments. For each comparison, we calculated the Bayesian factor, B_{-0} , which indicates the strength of evidence for the tested hypothesis (H1: effect is smaller in ASC group relative to the NT group) relative to the null hypothesis (H0: both group have equal effect size) using the JASP software (JASP Team 2020). For the perceptual measure, we also calculated the meta-analytic Bayes factor (Rouder and Morey 2011) using the data of the previous study (Takamuku et al. 2018). As a prior for expected effect size, we used the default Cauchy distribution with a scale factor of 0.707. A Bayesian factor below 1/3 was considered as evidence for the null hypothesis, whereas Bayesian factor above 3 was considered as evidence for the tested hypothesis. Any value between 1/3 and 3 was considered as insufficient evidence to draw a conclusion for or against either hypothesis.

Results

Inverse computation for visual perception

Figure 3 shows the measured PSE and JND in the two groups (both shown in terms of normalized movement frequency). The visual condition had a significant effect on the PSE ($F_{1,31} = 11.2, p = 2.13 \times 10^{-3}, \eta_p^2 = 0.27$), with a PSE of smaller movement frequency in the ‘pulling condition’ indicating that participants were biased in judging the velocity as expected. Neither the main effect of group ($F_{1,31} = 0.30, p = 0.58, \eta_p^2 = 0.0097$) nor the interaction between group and visual condition ($F_{1,31} = 0.72, p = 0.40, \eta_p^2 = 0.023$) were significant. Importantly, the main effect of visual condition was reliable in both the NT group ($t_9 = 2.5, p = 0.03, d = 0.83, CI = [0.002, 0.048 \text{ Hz/Hz}]$), and in the ASC group

($t_{22} = 2.3, p = 0.03, d = 0.49, CI = [0.001, 0.028 \text{ Hz/Hz}]$). The Bayesian factor was $B_{-0}(d_{rep}) = 0.71$ for the current study and $B_{-0}(d_{orig}) = 0.325$ for the previous study (Takamuku et al. 2018). The meta-analytic Bayesian factor was $B_{-0}(d_{orig}, d_{rep}) = 0.41$. Neither the group ($F_{1,31} = 0.05, p = 0.83, \eta_p^2 = 0.0$), the visual condition ($F_{1,31} = 1.74, p = 0.20, \eta_p^2 = 0.05$) or the interaction between the two factors ($F_{1,31} = 1.09, p = 0.30, \eta_p^2 = 0.03$) had a significant effect on the JND, i.e., the ability to distinguish the hand velocity.

Inverse computation for motor action

We first examined whether the hand and the object moved as expected. The motion of the object relative to the hand (phase delay and amplitude gain) did not differ between the two groups. The phase delay (mean \pm S.D.) was 78 ± 1.7 [deg] for the small delay condition and 97 ± 2.6 [deg] for the large delay condition. The gain in movement amplitude ranged from 1.04 to 1.12 among the four conditions. Meanwhile, analysis of the hand trajectory revealed that most participants tended to slow their hand movements in the visual feedback condition (values in Fig. 4a are greater than zero), and this effect was larger in some participants with autism.

Visual condition ($F_{1,33} = 18.9, p = 1.25 \times 10^{-4}, \eta_p^2 = 0.36$) and the interaction between group and visual condition ($F_{1,33} = 5.99, p = 0.02, \eta_p^2 = 0.15$) had a significant effect on the hand movement cycle (ANOVA with group, visual condition and load condition as factors; no other effects were significant). Hand slowing with visual feedback was observed in both groups (NT: $t_9 = 5.28, p = 5.10 \times 10^{-4}, d = 1.67, CI = [3.85, 9.63 \text{ ms}]$, **A S C** : $t_{24} = 5.45, p = 1.33 \times 10^{-5}, d = 1.09, CI = [15.0, 33.3 \text{ ms}]$), but the effect was significantly larger in the ASC group (NT vs ASC: $t_{33} = 2.45, p = 0.02, d_s = 0.92, CI = [2.93, 31.8 \text{ ms}]$). Correlations between the hand-slowing effect and measures of ASC are reported in section S4 in the Supplementary Information with linkage to abnormal eye contact (Fig. S4).

Our main objective in this study was to examine whether participants with ASC also show improvements in grip force control by observing the controlled object; the effect linked to inverse dynamics computation for motor control. In order to address this, we first controlled for the difference in the hand trajectory, since the load force pattern depended on the hand trajectory. To this end, we selected a matched subgroup of participants within the ASC group whose hand-slowing effect was comparable to those of the NT group (no significant difference from the mean of the NT group; distribution shown in Fig. 4a). This resulted in a subgroup of twelve ASC adults of which the age, gender and IQ did not differ from the NT group (section S2 in Supplementary Information).

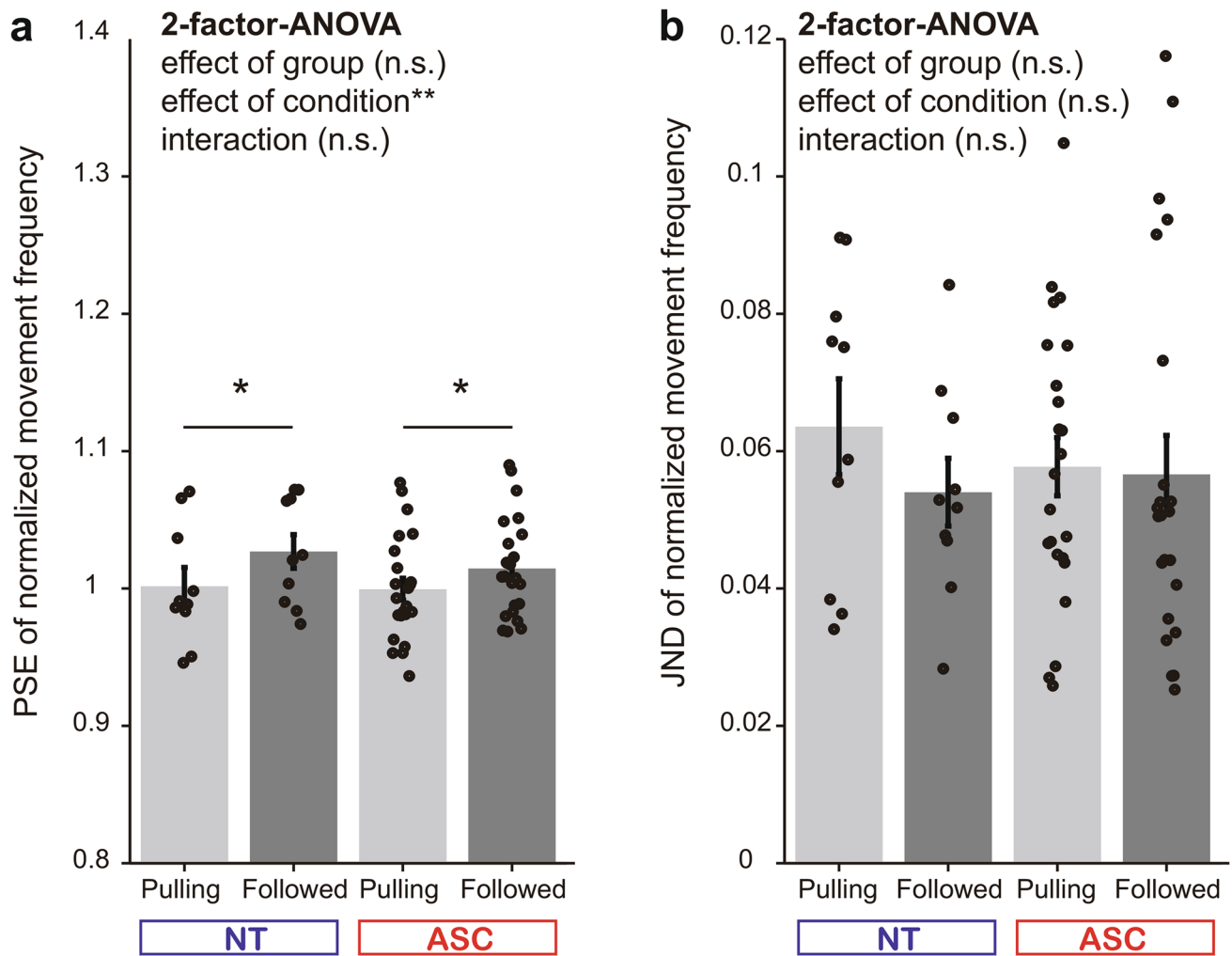


Fig. 3 Result of perception experiment. **a** and **b** show average PSE and JND for each group and condition, respectively. Black dots show data for each participant. Error bar denotes standard-error across participants. *denotes $p < 0.05$

Hand trajectory and load force pattern did not differ between the two groups (no statistically significant effect of group or its interaction to the amplitude or cycle of hand trajectory and load force pattern). Similarly, object motion relative to the hand (phase delay and gain in movement amplitude) also did not differ between the two groups (no effect of group or its interaction).

Figure 4b shows the grip force precedence relative to the load force pattern measured with and without visual feedback in the NT group, ASC subgroup and the ASC total group. Applying an ANOVA to the NT group and the ASC subgroup revealed main effects of the visual condition ($F_{1,20} = 50.0, p = 7.37 \times 10^{-7}, \eta_p^2 = 0.71$) and load condition ($F_{1,20} = 99.9, p = 3.18 \times 10^{-9}, \eta_p^2 = 0.83$), but neither the effect of group nor its interaction was significant ($p > 0.05$). Importantly, the grip precedence was significantly smaller with the visual feedback, not only in the NT group ($t_9 = 3.57, p = 6.00 \times 10^{-3}, d = 1.13, CI = [2.8, 12.7\text{ms}]$),

but also in the ASC subgroup ($t_{11} = 7.24, p = 1.66 \times 10^{-5}, d = 2.08, CI = [6.7, 12.5\text{ms}]$). When the magnitude of the effect was compared between the ASC subgroup and the NT group, the Bayesian factor $B_{-0} = 0.25$ was below $1/3$. One may argue that the reason why we did not find the difference between the two groups is because we selected the typical ASC participants. In order to address this concern, we also performed the same analysis between the NT group and the ASC total group. In this case, we found significant effects of visual condition ($F_{1,33} = 43.5, p = 1.69 \times 10^{-7}, \eta_p^2 = 0.57$), load condition ($F_{1,33} = 134, p = 3.61 \times 10^{-13}, \eta_p^2 = 0.80$) and the interaction between group, visual condition and load condition ($F_{1,33} = 5.70, p = 0.02, \eta_p^2 = 0.15$). The three-way interaction may be explained by the group difference in the hand-slowness effect, since the size of this effect correlates with the interaction between visual and load force conditions (see Fig. S5a in the Supplementary Information).

Importantly, the grip precedence was significantly smaller with the visual feedback in the ASC total group ($t_{24} = 6.73, p = 5.82 \times 10^{-7}, d = 1.35, CI = [6.5, 12.3\text{ms}]$). When the magnitude of the effect was compared between the ASC total group and the NT group, the Bayesian factor $B_{-0} = 0.24$ was below $1/3$. We also found that there is no statistically significant correlation between the hand-slowing effect and the improvement in grip timing (Fig. S5b in the Supplementary Information). This was also the case in the earlier study (Takamuku and Gomi 2019) and suggests that the two effects of visual feedback, one on grip control and another on arm control, are independent. Finally, while our analysis focused on the asynchrony between the two forces, further analysis of the grip-load force coupling did not reveal any evidence for deteriorated ability of the inverse computation (see section S6 in the Supplementary Information). Taken together, our results suggest that the inverse computation for motor action is also preserved in the ASC participants.

Discussion

Autistic and matched neurotypical adults participated in two experiments, a perception experiment and a motor experiment, each examining the use of the inverse dynamics computation for sensory perception and motor action, respectively. In both tests, the fundamental sensorimotor bias linked to the inverse computation was observed not only in the typical adults but also in the autistic adults. Furthermore, Bayesian factor analyses suggested that the bias linked to the inverse computation for motor control was comparable between the two groups. This suggested that adults with autism are capable of inverse dynamics computation in contexts of both sensory perception and motor control, and the ability is comparable to the typicals at least in the latter context. However, some autism participants showed atypical hand slowing with the visual feedback in the motor task, which suggests that other visual-motor difficulties may affect these participants. These results have important implications on how adults with autism use visual feedbacks and internal models for shaping their motor actions.

In the perception experiment, we measured the perceptual bias caused by seeing a situation with complex dynamics (a hand pulling a car) compared to the same two objects moving with no physical link between them. The bias was detected both in the NT and the ASC group with comparable magnitude. This replicated the earlier finding (Takamuku et al. 2018) with a completely different group of participants (different country/group) and suggests that the participants in our study also had preserved ability to use the inverse dynamics computation for sensory perception. One may wonder whether the two

excluded participants, both in the ASC group, represent a subpopulation of autistic adults with perceptual diversity. However, the ratio of excluded participants in this task were comparable between the two groups when we also considered the previous study (NT: 7/36, ASC: 9/52; $z = 0.26, p = 0.38 > 0.05$), and did not provide any evidence of atypical perception specific to ASC.

The main objective of our study was to examine whether the autistic adults also show preserved ability of inverse dynamics computation for motor action. This was tested in the motor experiment by measuring the improvement in grip timing caused by seeing the controlled object; an effect linked to the inverse dynamics computation for motor action (Takamuku and Gomi 2019). The improvement was detected both in the NT group and the ASC group, irrelevant of whether the difference in hand trajectory was controlled or not. This suggests that the inverse dynamics computation for motor action is also preserved in adults with autism.

Our finding contrasts with the earlier findings that people with autism rely less on visual feedback in acquiring (Marko et al. 2015) and representing (Haswell et al. 2009) internal models for force field adaptation. Importantly, the autism participants showed no evidence of internally representing the force field in visual coordinates (evidence based on generalization pattern). This suggested a possibility that they failed to relate the cursor motion with the applied force. However, all our experiments including those in our previous study consistently suggested that adults with autism can extract force information from visual motion signals. One difference between the adaptation studies and our study is the age of the participants. Children around the age of 10 participated in the adaptation studies, whereas all our participants were above 20. Earlier study suggested that difference in volume of cerebellar vermis between ASC and NT decreases with age (Hashimoto et al. 1995). Considering that the vermis consists a major part of the sensorimotor cerebellum (Buckner et al. 2011) that Marko et al. linked to the abnormality in force-field adaptation, the difficulty in the inverse computation could be limited to an early age. Another possibility is that the autistic participants had normal ability of the inverse computation but did not rely on it for force-field adaptation. As mentioned earlier, the adaptation can also be driven based on proprioceptive signals. Haswell et al. pointed out that the overgrowth of short-range connection between motor and somatosensory regions, observed in children with autism (Mostofsky et al. 2007), may have lead them to rely more strongly to proprioception than vision, i.e., less use of vision results from overuse of proprioception.

An unexpected finding in our motor experiment was that some participants with autism tended to slow down their hand movement when visual feedback of the object was available, and the effect was larger than the controls.

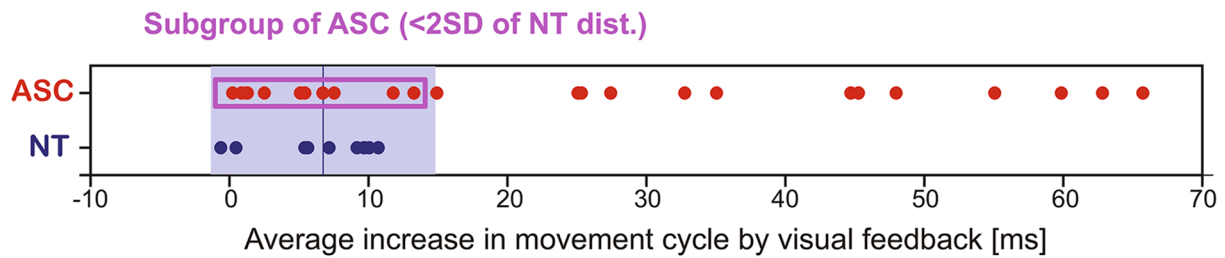
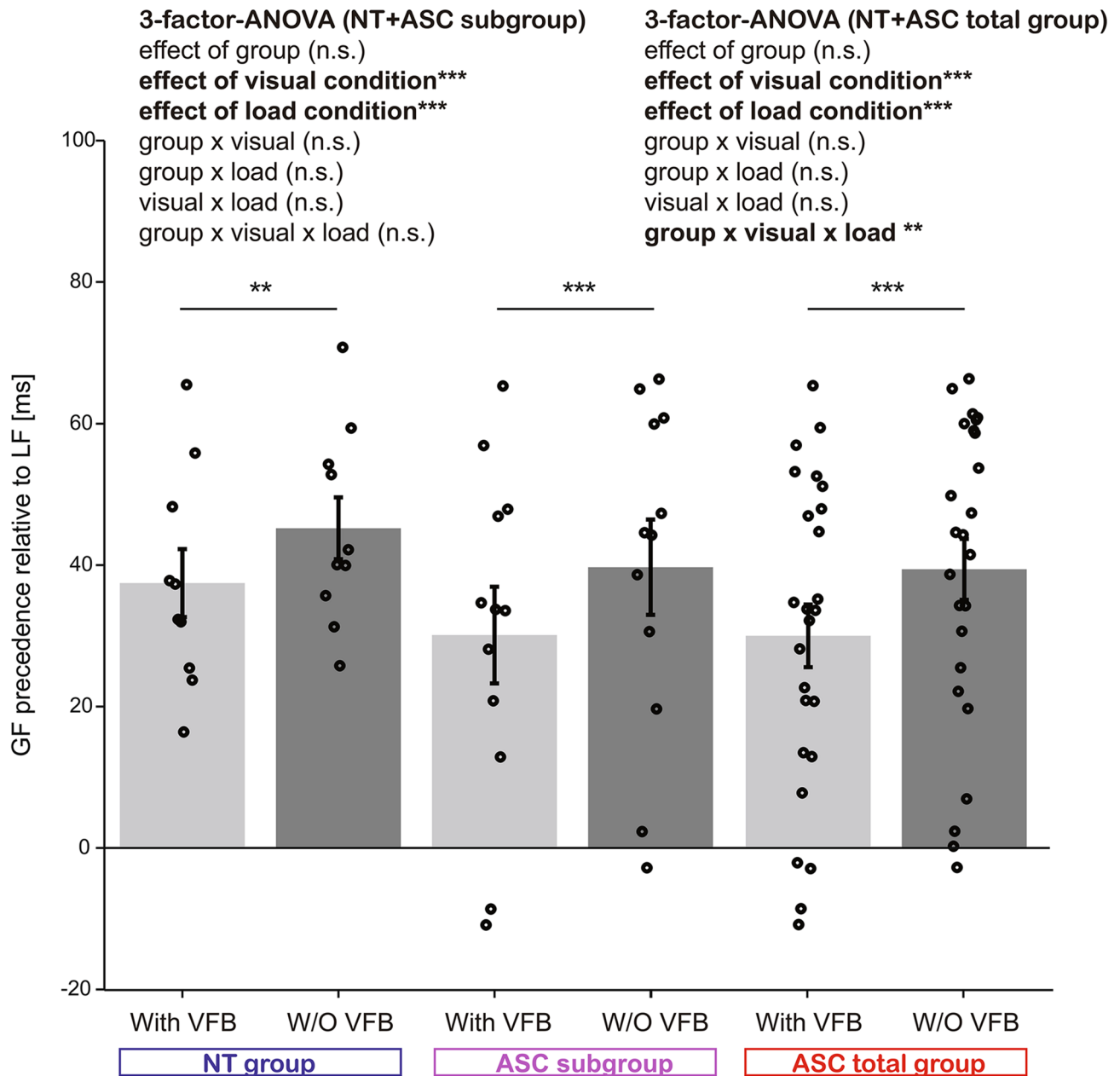
a**b**

Fig. 4 Result of motor action experiment. **a** Distribution of average increase in movement cycle by visual feedback for ASC and NT group. Each dot represent data for each participant. Area colored in blue are within 2 SD for NT distribution. Purple square indicate data of ASC subgroup. **b** Grip force precedence with and without visual feedback in NT group, ASC subgroup and ASC total group. Error bars denote standard error across participants and circles indicate data for each participant. Load force condition is collapsed in the figure, but used for analysis. ** and *** indicate $p < 0.01$ and $p < 0.001$, respectively

The effect might reflect an abnormality in visual control of reaching movements. Glazebrook et al. (2009) showed that reaching movements slow down with visual feedback of hand position in participants with autism, although this was not replicated in a recent study (Fukui et al. 2018). Another possibility is that the larger hand-slowing effect in participants with autism resulted from their difficulty in attention control. Earlier studies have suggested atypical attention control in people with autism (Allen 2001) which is also linked to abnormal eye contact (Neumann et al. 2006). This may have made it difficult for them to disregard the visual feedback and follow the periodic beep which specified the movement cycle.

It remains unclear why the visual feedback caused the hand to slow. One possibility is that it resulted as a consequence of optimal feedback control (Scott 2004; Todorov 2004) in which the state of the arm is estimated using the visual feedback and motor output is determined based on the estimated state. In our study, the visual feedback of the object was similar to a delayed visual feedback of the hand position. This may have delayed the estimated state and consequently have delayed the motor output. It should be noted, however, that such delay in motor output is unlikely to explain the improvement in grip timing for several reasons. First, correlation between the hand slowing effect and the improvement in grip timing has never been found; neither in the current study (Fig. S5b), our previous study (Takamuku and Gomi 2019), nor in the study by Sarlegna et al. (2010). Secondly, Sarlegna et al., showed that delaying the visual feedback can precede the grip force pattern; an effect in the direction opposite to what would be expected from the optimal control theory. Finally, in the ASC group of our study, visual effect on the hand movement was atypical, whereas the effect on the grip force control was intact.

The typical and atypical visuomotor control of grip and arm movements have important implications on the use of visual feedback in adults with autism. Although some studies suggested that people with autism may be insensitive to dynamic visual feedbacks (Masterton and Biederman 1983; Gepner et al. 1995), we did not find any evidence to support such hypothesis. Our study suggests instead that abnormality in use of visual feedback depends on the specific context, and that visual processes

that underlie the grip-timing effect such as detecting the visual motion, identifying the dynamics of the observed system, and mapping the observed motion to force information are all intact.

To conclude, our study suggests preserved ability of inverse dynamics computation, not only for sensory perception, but also for motor action in adults with autism. Namely, they seem to be capable of seeing forces in visual motion just like the neuro-typical adults, at least when the observed system involves a simple inertial dynamics. While many studies have examined the use of forward models in autism (Schmitz et al. 2003; Gowen and Miall 2005; Blakemore et al. 2006; David et al. 2009), our study provides unique evidence on the use of the inverse computation for motor control in this population. An interesting question is whether the conclusion also applies to the inverse computation from biological motion; an ability required for instance to infer the weight lifted by others from their motion (Runeson and Frykholm 1981) or to mimic the exact body action of others. The issue will be addressed in future studies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00221-021-06046-3>.

Acknowledgements This study was supported by Grants-in-Aid for Scientific Research (JP16H06566) from Japan Society for the Promotion of Science. We thank Prof. Nobumasa Kato, Dr Makio Kashino, Dr Ryu-ichiro Hashimoto, Dr Chihiro Itoi for their assistance and all the participants for their contribution to the study.

Author contributions ST and HG conceived and planned the experiment in consultation with all the other authors. ST collected the behavioural data and CK collected the ADOS data. ST analysed the data and wrote the first draft. All authors contributed to the final approved draft.

Funding This study was supported by Grants-in-Aid for Scientific Research (JP16H06566) from Japan Society for the Promotion of Science.

Data availability The data supporting the findings of this study are available within the article and the supplementary materials.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

Ethical approval Recruitment of participants and experimental procedures were approved by the Ethics Committee of NTT Communication Science Laboratory as well as Showa University and were conducted in accordance with the Declaration of Helsinki.

Informed consent to participate All participants gave informed consent before participating in the study.

Informed consent for publication All participants signed informed consent regarding publishing the data.

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