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Motor Abilities in Autism: A Review Using a Computational Context

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Abstract Altered motor behaviour is commonly reported in Autism Spectrum Disorder, but the aetiology remains unclear. Here, we have taken a computational approach in order to break down motor control into different components and review the functioning of each process. Our findings suggest abnormalities in two areas—poor integration of information for efficient motor planning, and increased variability in basic sensory inputs and motor outputs. In contrast, motor learning processes are relatively intact and there is inconsistent evidence for deficits in predictive control. We suggest future work on motor abilities in autism should focus on sensorimotor noise and on higher level motor planning, as these seem to have a significant role in causing motor difficulties for autistic individuals.

Keywords Autism · Motor control · Sensorimotor integration · Prediction · Motor learning

Introduction

Although sensory and motor impairments in Autism Spectrum Disorder (ASD) are not considered to be core features of autism, there is increasing acknowledgment that they are nevertheless highly prevalent and can have a significant impact on quality of life and social development. The current review examines motor control in autism, within a framework derived from computational models of the motor system, and with a focus on whether specific stages of motor computation are abnormal.

Motor abnormalities in ASD can be observed in infancy (Brian et al. 2008; Provost et al. 2007; Teitelbaum et al. 1998; although see Ozonoff et al. 2008) and are apparent throughout childhood and into adulthood (Fournier et al. 2010; Ming et al. 2007; Van Waelvelde et al. 2010). A number of different motor deficits have been observed using standardized test batteries (Table 1) and the prevalence of such deficits has been reported to be between 21 and 100 % (Ghaziuddin et al. 1994; Green et al. 2002; Manjiviona and Prior 1995; Miyahara et al. 1997; Pan et al. 2009), highlighting that motor impairment is a significant but potentially variable aspect of ASD. As acquisition of good motor skills is important for a range of everyday abilities such as communication and language development (Gernsbacher et al. 2008), playing and interacting with others (Clearfield 2011), mental imagery (Williams et al. 2008) and perception (Blaesi and Wilson 2010; Eskenazi et al. 2009; Wilson and Knoblich 2005), it is likely that abnormal development of motor control can have far reaching consequences on development (Leary and Hill 1996). For example, it has been shown that motor ability is correlated with daily living skills in autistic children (Jasmin et al. 2009) and that better motor control is related to decreased severity of ASD in later life (Sutera et al. 2007). Therefore, increasing our understanding of the aetiology of motor deficits in ASD is a crucial step towards treating and preventing this potential developmental cascade.

Our current understanding of motor function in autism is limited in two ways. First, it is unclear if there are certain motor problems which are specific to autism (as opposed to other developmental disorders). For example, motor

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Table 1 Motor signs observed in autism using standardized test batteries. Numbers refer to test batteries used

	Studies reporting motor sign
Fine motor signs	
Slower repetitive hand and foot movement	Dowell et al. (2009)[4], Dziuk et al. (2007)[4], Freitag et al. (2007)[2], Jansiewicz et al. (2006)[4]
Slower and less accurate manual dexterity	Green et al. (2002)[1], Manjiviona and Prior (1995)[1], Miyahara et al. (1997)[1]
Diadochokinesis	Freitag et al. (2007)[2]
Poorer ball skills (e.g., aiming and catching)	Green et al. (2002)[1], Manjiviona and Prior (1995)[1], Miyahara et al. (1997)[1], Pan et al. (2009)[3], Staples and Reid (2010)[3]
Gross motor signs	
Un-stable balance	Freitag et al. (2007)[2], Green et al. (2002)[1], Jansiewicz et al. (2006)[4], Manjiviona and Prior (1995)[1], Miyahara et al. (1997)[1]
	Studies using quantitative methodology: Gepner et al. (1995), Kohen-Raz et al. (1992), Minshew et al. (2004), Molloy et al. (2003)
Impaired gait (e.g., tandem gait, heel or toe walking)	Jansiewicz et al. (2006)[4], Ming et al. (2007)[5]
Reduced coordination of locomotor skills (e.g., running and jumping)	Pan et al. (2009)[3], Staples and Reid (2010)[3]
Other	
Hypotonia	Ming et al. (2007)[5]

The Movement Assessment Battery for Children (MABC; Henderson and Sugden 1992)[1], The Zurich Neuromotor Assessment (ZNA; Largo et al. 2002)[2]; The Test of Gross Motor Development (TGMD-2; Ulrich 2000)[3], The Physical and Neurological Examination of Subtle Signs (PANESS; Denckla 1985)[4] and retrospective and neurological examination[5]

deficits are observed in Developmental Coordination Disorder (DCD) and Attention Deficit Hyperactivity Disorder (ADHD), but it is not known if these are similar to the motor deficits in autism (Dewey et al. 2007; Green et al. 2002; Ozonoff et al. 2008; Provost et al. 2007). It is also unclear whether there are differences in motor ability between individuals diagnosed with different forms of ASD such as Asperger's or autism (Ghaziuddin et al. 1994; Jansiewicz et al. 2006; Manjiviona and Prior 1995; Rinehart et al. 2006a, b). Second, commonly used clinical and standardized measures of motor performance such as those in Table 1, do not always provide much information about the underlying motor processes. For example, test batteries may distinguish "fine" motor skills involving manual dexterity and visuomotor control from "gross" motor skills involving walking or throwing, and may consider posture or balance as separate categories. While these categories may be helpful in considering how an individual needs support in daily life, they do not relate closely to the underlying motor mechanisms. Fine motor skills encompass a number of different processes relating to sensory, planning and execution aspects of motor control whereas balance and posture may actually share some aspects such as integrating different senses and predicting sensory consequences of movement. Thus, it is often hard to know which specific motor processes are abnormal in autism. Understanding motor difficulties in autism in terms of specific computational mechanisms may allow clearer

distinctions between different developmental disorders and has the potential to reveal if and how poor motor skills might be causally related to poor social skills. A better understanding of the origins and nature of motor difficulties in autism will also contribute to better training and intervention methods and is well suited to tackling the issues of heterogeneity within the autistic spectrum.

In recent years, studies of motor systems in typical adults have given rise to sophisticated computational models of the different control and feedback processes required for accurate everyday movement (Jordan and Wolpert 1999; Wolpert and Ghahramani 2000) (Fig. 1). However, these models have rarely been applied to developmental motor disorders (Sanger 2003). Our aim in this review is to determine how the component processes identified in computational models can be mapped onto the developmental dysfunction of motor systems seen in autism. We base our review on a model advanced by Wolpert and colleagues (Wolpert 1997), which incorporates Optimal Control Theory (Diedrichsen et al. 2010) and provides a flexible framework within which to examine a number of different motor processes. There are other models of motor control, for example, Dynamical Systems Theory (Kelso 1995) suggests that behavior arises from the dynamics of coupled oscillators, while theories of motor synergies examine how different muscle groups work together as functional units (d'Avella and Bizzi 2005). We have chosen to focus on the model from Wolpert and colleagues
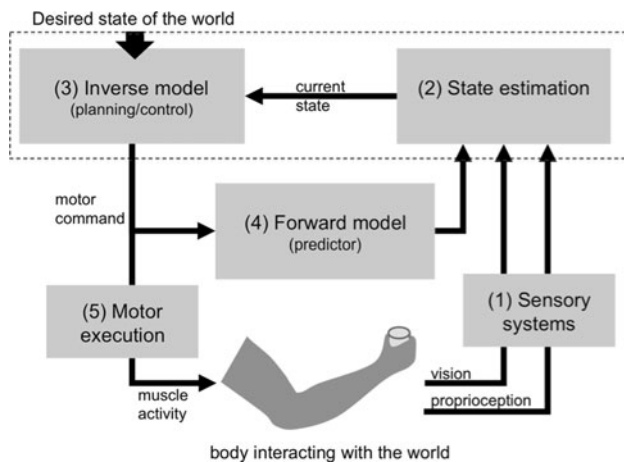
Fig. 1 Different computational processes involved in motor control. Information from different senses is integrated to form a state estimate of the current location of the body and surrounding environment (*1*, *2*). This state estimate is used by the inverse model to plan a movement to obtain the desired state (*3*). The resulting motor command is used by the forward model to predict the motor and sensory outcome of the intended movement and compared to the actual sensory state to check for errors (*4*). The motor plan is converted into muscle activity in order to execute the movement (*5*) and sensory feedback used to update the state estimate. *Dashed line* indicates processes involved in sensorimotor integration

because it has a broad scope, covering many different motor functions and proposing distinct computational units which can potentially be linked to different cognitive tasks.

In the current review we attempt to bring together those studies that focus on particular motor computations in ASD, with emphasis on quantitative experimental procedures. As we have specifically selected those articles that fall within the framework of the computation model in Fig. 1, our review is not intended to be a comprehensive summary of all previous motor studies in ASD. There are three main sections. Firstly, we briefly discuss the different processes identified in typical adult motor control. Then we review whether there is evidence for involvement of each of these processes in autistic motor ability. Finally, we draw together some conclusions and suggest approaches to move forward our understanding of motor control in ASD.

Brief Overview of Motor Control Processes

Consider the simple task of reaching your hand out to pick up a mug of tea. Figure 1 provides a summary of the basic motor control processes involved (Shadmehr and Krakauer 2008; Wolpert and Ghahramani 2000), and the numbers in this description refer to the components of the figure. First, sensory inputs from the visual system and the proprioceptive system provide essential information about the task, including an image of the mug on the table and a

sense of your hand in space (1). These different sensory inputs must be integrated into a unified *state estimate* which specifies where the mug is, how big it is, where your hand is and other task-relevant information (2). The estimate of the current state of the world must next be compared to the desired state—'my hand is by my side; I want the hand on the mug'—and the motor system must plan how to move your hand smoothly and efficiently from its current location to the mug. This planning process is also termed the *inverse model* because it solves the inverse problem of how to convert a goal (hand-on-mug) into a sequence of motor commands (3). This sequence of motor commands can then be executed by the body (5).

However, during execution, errors may arise due to planning failure, external perturbations or inherent noise within the motor system. Sensory feedback is too slow to allow efficient error correction in rapid hand movements, as it takes at least 165 ms to detect and correct errors (Young and Zelaznik 1992). To reduce this problem, the brain uses a *forward model* (4) which takes a copy of the outgoing motor command (efference copy) and generates a prediction of the expected sensory input. As the movement progresses, the actual sensory input is compared to the predicted input to allow rapid detection and correction of errors. In this way, it is possible for the hand to accurately move to the mug of tea and grasp it appropriately. A core process within this model is *sensorimotor* integration, which is defined as integration of forward model output with the state estimate as well as the use of the state estimate by the inverse model to create a motor plan (dashed lines in Fig. 1).

In everyday behaviour, this motor circuit functions in a highly integrated manner, as almost all tasks make use of all the different components. Similarly, the numbering of the circuit components does not necessarily reflect the order of the different processes: aspects of the inverse model may already be planned prior to the estimation of the current state. This means that it is challenging for the psychologist to separate the different motor computations. However, it is possible to find tasks which load more or less heavily on different components. For example, when preparing to pick up a knife and cut an apple, you must plan (3) how your hand should approach the knife to grip the handle ready for cutting, rather than gripping the blade. Here, the correct inverse model for planning how and where to grip the knife is an essential element. However, when picking a raspberry, it is important to grip with just enough strength to pull it from the plant without crushing the delicate berry (Wolpert and Ghahramani 2000). In this case, an inverse model (3) would initially plan the reach and grip of the raspberry, but a forward model (4) of the predicted grip strength is essential to fine tune the grip and prevent the berry falling or being crushed. Thus, studies of

participant's performance on different functional tasks can inform us about the relative integrity of the different components of the motor circuit.

Two further critical processes are not illustrated in Fig. 1. First, motor control systems are not fixed at birth, but rapidly and continually learn new information and adapt to the environment. This motor learning takes place on all timescales and in all components of the motor circuit. For example, a lady who puts on a heavy bracelet must adapt to the additional weight on her arm over a few minutes. This learning involves updating the forward model (4) because with a heavy bracelet on, the same muscle activity results in less arm movement. The lady must also plan her actions to take into account the extra weight (3), and pay more attention to proprioceptive information (2) from her arm until she has grown accustomed to the bracelet. Similar processes allow the growing child to learn how his limbs grow in length and mass over the lifespan. The term *motor learning* covers all these changes, as well as more abstract learning about using tools and sequencing actions. In the present review, we focus mainly on adaptation of the motor model in response to changes within the environment or body dynamics. We leave aside the literature on learning to use tools or learning to sequence actions although we do examine how well autistic people are able to perform these aspects of planning. Second, Fig. 1 does not show how motor processes are organized hierarchically. For example, the goal of baking a cake is accomplished by breaking it down into sub-goals (crack the eggs, sieve the flour, …) which each involve a sequence of motor steps (lift the egg, move to bowl, …) and each step is implemented by a sequence of kinematic movements (close fingers, lift hand …) (Berstein 1967; Botvinick 2008; Grafton and Hamilton 2007; Jordan and Wolpert 1999). The simple computational framework outlined in Fig. 1 can be subsumed within a broader hierarchical framework, in which the forward and inverse models which implement basic movements are themselves controlled by higher lever forward-inverse models responsible for sequencing of movements (Haruno et al. 2001). The detail of this approach is beyond the scope of the current paper, but we will consider if potential motor difficulties in autism arise from lower levels of the motor system (e.g., control of individual finger movements) or higher levels (e.g., sequencing of actions).

Finally, tentative efforts have been made to localize different components of motor processing to different brain regions, but we will not consider these localisations here. Similarly, space constraints preclude the discussion of motor related processes such as observational learning and imitation, which have been considered extensively elsewhere (Hamilton 2009: Gallese et al. 2009; Williams et al. 2004b). Almost all of the studies include high functioning autistic individuals so we are not able to comment specifically on motor functioning in lower functioning groups. However, the model serves as a useful starting point for focusing on those processes that are considered the most basic and fundamental to motor control. A more detailed knowledge of how these essential motor components function in autism will provide good grounding for further understanding higher level skills such as imitation. We consider here the evidence for the integrity of each of the 5 components of Fig. 1 in order and Table 2 gives a summary of this evidence.

(1) Sensory Systems

Precise motor performance requires accurate sensory inputs concerning the body and the world. We focus here on vision, touch and proprioception because these are most important for movement. Difficulties in sensory systems could arise at different stages. First, the brain must receive the raw input signals from the eye and from skin and joint receptors without excess noise or error. Second, these signals must be interpreted, for example, transforming the retinal image into a representation of hand location. Integration across different senses is considered in the next section.

Data on basic sensory processing in autism presents a mixed picture. Questionnaires and individual reports often describe altered sensory experiences such as hyper- and hypo-sensitivity across all modalities in autism (Baranek et al. 2006; Crane et al. 2009; Harrison and Hare 2004; Kern et al. 2006; Leekam et al. 2007). For example, both autistic children and adults are more likely to display or report greater discomfort in response to visual or tactile stimuli and avoid situations where they may encounter such stimuli. There is also much intra and inter-subject variability in terms of both the nature and degree of these sensory experiences (Crane et al. 2009). More quantitative visual studies indicate relatively intact low level functions such as flicker and static contrast sensitivity (Bertone et al. 2005; de Jonge et al. 2007; Pellicano and Gibson 2008; Pellicano et al. 2005). Detection of tactile stimuli and discrimination between different textures also appears not to differ between autistic and neurotypical participants (O'Riordan and Passetti 2006). Moreover, it has been reported that autistic individuals show better detection and localization of low level vibrotactile stimuli then neurotypical individuals (Blakemore et al. 2006; Cascio et al. 2008; Tommerdahl et al. 2007).

Fuentes et al. (2011) recently reported similar levels of proprioceptive ability in twelve adolescent autistic children and twelve matched controls. These children carried out three different tasks where they were asked to match a

Table 2 A summary of motor studies of autism which test specific computational processes. Sensory processing has been been omitted due to the large number of studies on this topic (see text for details). Grey shading indicates the behavior of autistic participants differs from controls. Effect sizes (d) are given where possible. Mean age and full scale IQ are given with standard deviation or range unless otherwise stated. Control = neurotypical comparison group, MLD = Moderate learning difficulties comparison group, N = number of participants, FS = full scale IQ, VMA = verbal mental age, PIQ = performance IQ

Paper	Participants	Task	Findings	Motor processes tested
Foss-Feig et al. (2010)	*Autism:* N = 21; Age = 12.6 ± 2.6; IQ = 108.5 ± 18.7 *Control:* N = 17; matched on sex, age, IQ (FS/V/P)	*Flash-beep illusion:* Participant reports number of flashes seen while auditory beeps are presented at a similar time to flash. The addition of multiple beeps in conjunction with the flash often results in an illusory perception of additional flashes. The time window of integration can be examined by changing the relative timing of the flashes and beeps	Autistic children were more affected by the beep (reporting more illusionary flashes) and over a larger time window	2 (*state estimation*)
Kwakye et al. (2011)	*Autism:* N = 16; Age = 12.2 ± 2.7; IQ = 102.9 ± 18.7 *Control:* N = 14; matched on sex, age, FSIQ	*Temporal order judgment task* (auditory-visual). Participant reports which of two circles appeared first. The addition of beeps in conjunction with the circles aids temporal order judgment. This improvement decreases with increasing temporal asynchrony between the beeps and circles	Autistic children benefitted more than controls to the addition of beeps and over a larger time window	2 (*state estimation*)
Taylor et al. (2010)	*Autism:* N = 24; Age = 12.6 ± 2.4; VMA = 11.5 ± 3.1 *Control:* N = 30; matched on sex, age, VMA	*McGurk effect:* Participants view videos of a speaker, which have been dubbed. For example, they see "Ga", but hear "Ba" giving the illusionary impression that "Da" has been spoken	Autistic group showed smaller McGurk effect which increased to control levels with increased age	1 (*sensory inputs*) 2 (*state estimation*)
Hughes (1996)	*Autism:* N = 36; Age ~ 13 ± 3; VMA = 8.64 ± 2.5 (High group); 5.5 ± 1.4 (Low group) *MLD:* N = 24; Age ~ 11 ± 3; VMA = 6.9 ± 1.4 (High group); 5.6 ± 1.1 (Low group) *Control:* N = 28; Age ~ 3.5 ± 0.2; VMA = 4 ± 0.2 (High group); 3.3 ± 0.3 (Low group) Groups not consistently matched	*Grip Selection task:* Participants are asked to grip and lift a bar and place it vertically on a circular target area. In Fig. 2 the participant must place the pale half on the target. If participants plan for the end state, they should more frequently start in the awkward underhand posture and end in the comfortable overhand posture. Alternatively, they could start with the comfortable overhand posture and end in the awkward underhand posture, which would indicate lack of planning	Autistic children more frequently ended in the uncomfortable posture then the MLD and control group	3 (*planning*)
Van Swieten et al. (2010)	*Autism:* N = 20; Age = 9–14 years; IQ = 95.7 ± 14.2 *Control:* N = 44; Age = 9–14 years; IQ = "normal VMA" Unclear whether matched on any parameter	*Grip Selection task:* see above	Autistic and control children had equivalent planning abilities, choosing to end more frequently (approx 80 % of trials) in comfortable position	3 (planning)

Table 2 continued

Paper	Participants	Task	Findings	Motor processes tested
Hamilton et al. (2007)	*Autism:* N = 25; Age = 8.1 ± 1; VMA = 4.3 ± 1 *Control:* N = 31; Age = 4.1 ± 0.7. Matched on VMA	*Grip Selection task:* see above	Both control and autistic children performed a significant and similar number of planning errors	3 (planning)
Cattaneo et al. (2007)	*Autism:* N = 8; Age = 6.2(5.2–11.9); IQ = 98 ± 12.4 *Control:* N = 8; Age = 6.5(5.2–11.9); IQ = 104.7 ± 7.7. Matched on age and IQ	*Action chaining:* Children were instructed to reach and grasp a piece of food to bring to the mouth to eat or to place into a container. Muscle activity of the mouth opening Mylohyoid was recorded using EMG	In contrast to placing the food in a container, EMG activity was present during the reach and grasp components as well as when bringing the food to the mouth in the control children, showing anticipatory activity. EMG activity in the autistic children was only present when bringing the food to the mouth	*3 (planning)*
Fabbri-Destro et al. (2009)	*Autism:* N = 12; Age = 10 ± 2.3; IQ = 84.3 ± 11.3 *Control:* N = 14, Age = 7.6 ± 2.1; IQ = not given. Matched on Ravens Progressive Matrices	*Action chaining:* Children were instructed to reach and grasp an object, then place it into a container. Trials varied according to whether the container was small or large. Reaching time to grasp the object and time for placing the object into the container were calculated	For the control children, both reach and placing times were longer for the small container condition. However, only the placing times were longer for the small container condition in the autistic group, suggesting lack of motor action chaining	3 (planning)
Mari et al. (2003)	*Autism:* N = 20; Age = 10.5 ± 1.5; IQ = 70–109 *Control:* N = 20; Age = 10.4 ± 1.4; IQ = 70–109. Matched on age and sex. Mean IQ not given	*Reach-to-grasp task:* Participants were instructed to reach and grasp either a small (1 × 1 × 1 cm) or large (4 × 4 × 4 cm) block, positioned at either 18 or 28 cm away from the participant. Movements were recorded with an infrared tracking device	A dichotomy between a low ability (IQ 70–79) and normal/high ability (IQ 80–109) group was found. The former group showed a longer movement duration and deceleration time, lower amplitude of peak velocity and the grasp onset was delayed compared to the controls. The higher functioning group demonstrated shorter movement duration and higher amplitude of peak velocity in contrast to the controls	3 (planning)
Glazebrook et al. (2006)	*Autism:* N = 9; Age = 26.9 ± 6.8; IQ = 92 ± 21 *Control:* N = 9; Age = 25.1 ± 5.1; IQ = not performed Matched on age	*Reaching to different sized targets:* Participants were instructed to point to circular targets (either 1 cm or 2 cm) at different distances to give five different indexes of difficulty (3; 3.41; 4; 4.41; 5). Movements were measured with an infrared Optotrak	Autistic participants modulated their movements according to index of difficulty, although the following differences between the two groups was found. RT and movement time was longer for autistic participants compared to controls, particularly for the longer movements (d = 1.4, 1.7 respectively). Compared to the control participants, the autistic group showed lower peak acceleration and peak velocity, particularly for longer movements (d = 1.1, 1.3 respectively). Time to peak velocity was more variable for the autistic than control group and spatial variability at peak acceleration and peak velocity were also more variable for the autistic participants	3 (planning), 5 (execution)

Table 2 continued

Paper	Participants	Task	Findings	Motor processes tested
Glazebrook et al. (2008) (Exp 1)	*Autism:* N = 18; Age = 23.7 ± 7.9; IQ = 88 ± 18.2 *Control:* N = 18; Age: 20.6 ± 4.5; IQ = not performed Unclear whether matched on any parameter	*Reaching with precues:* Participants placed each index finger on two middle buttons. Either side of these "home" buttons were four target buttons. Participants were instructed to reach for a target button once illuminated. Prior warning regarding direction (left/right), extent (far/near) or hand (right/left) was given in the form of precues (illumination of the target buttons)	Both groups reacted faster in the presence of precues. Movement time was unaffected by precues in the control group, but the autistic group had slower movement times when hand and extent were known	3 (planning),
Schmitz et al. (2003)	*Autism:* N = 8; Age = 7.9 ± 1.3; IQ = >70 *Control:* N = 16; Age = 6 ± 1; IQ = not performed Unclear whether matched on any parameter	*Bimanual load lifting:* A load (weight) was attached to the participants left arm. In the voluntary unloading they were required to take the load off their left arm, using their right arm. In the imposed unloading trials, the experimenter took the load off the participants left arm. EMG recorded muscle activity from the left biceps, which usually shows a pattern of inhibition during voluntary unloading. A potentiometer recorded the upward movement of the arm during unloading	During voluntary unloading, inhibition of activity for the biceps occurred prior to unloading in the control participants, indicating an anticipatory response. However, this pattern of activity occurred during unloading for the autistic group (d = 2.5). The upward movement of the left arm also occurred earlier with a shorter duration for the control compared to autistic group	*4 (prediction)*
Gowen and Miall (2005)	*Autism:* N = 12; Age = 27.4 ± 11.1; IQ = 104 ± 22.1 *Control:* N = 12; Age = 28.2 ± 11.7; IQ = 112.4 ± 15.9 Matched on sex, age and IQ	*Grip force:* Participants gripped a device containing a force sensor and accelerometer between thumb and index finger and lifted it up and down for three trials of 10 s	No significant differences between the two groups on mean modulation of movement, mean and standard deviation of force and mean phase difference between grip and load force	4 (prediction), *5 (execution)*
David et al. (2009)	*Autism:* N = 13; Age = 11.2 ± 3.4; IQ = 91.7 ± 19.5 *Control:* N = 13; Age = 10.8 ± 3.1; IQ = not performed Matched on age and sex	*Grip force:* Participants were instructed to pick up a device containing a force sensor and accelerometer between thumb and index finger and place it on a target area. There were 15 trials with 3 different weights	Grip to load force latency was longer for autistic participants (d for 3 different weights: 0.7, 0.38, 1.33) and grip force higher (d for 3 different weights: 0.7, 0.5, 0.47)	*4 (prediction)*
Blakemore et al. 2006 (Exp 2)	*Autism:* N = 16; Age = 27.3 ± 12; IQ = 109.2 ± 24.1 *Controls:* N = 16; Age = 33.9 ± 12.5; IQ = 112.8 ± 11.2 Matched on age	*Self or externally produced tactile sensitivity ratings:* The palm of the participants hand was touched with a piece of foam that was either moved by the participant or the experimenter. The participant rated the tickliness of the foam	The foam was rated as more tickly in both groups when moved by the experimenter	4 (prediction)

Table 2 continued

Paper	Participants	Task	Findings	Motor processes tested
Glazebrook et al. (2009)	*Autism:* N = 13; Age = 23.4 ± 4.5; IQ = 79.4 ± 14.5 *Control:* N = 15; Age = 23.4 ± 3.2; IQ = not performed Unclear whether matched on age or IQ	*Reaching movements:* Participants were required to perform 20 cm horizontal reaching movements to either a predictable or unpredictable target. In a second part, the participants performed reaches without visual feedback. Movements were recorded with an infrared Optotrak	When vision was present, the autistic participants exhibited slower RT's (d = 2.7) and longer, less accurate (d = 1.2) movements. They showed greater spatial variability for peak acceleration, peak velocity and peak deceleration but similar variability to the control group for the end point. Autistic participants also made significantly longer reaches in the vision absent condition compared to the control groups	5 (*execution*)
Gidley Larson et al. (2008)	(*Exp1*) *Autism:* N = 20; Age = 10.9 ± 1.8; PIQ = 110 ± 14.9 *Control:* N = 16; Age = 10.8 ± 1.3; PIQ = 112.8 ± 11.6 (*Exp 2*) *Autism:* N = 15; Age = 11.1 ± 1.6; PIQ = 108.9 ± 15.6 *Control:* N = 10; Age = 11.7 ± 1.5; PIQ = 117 ± 12 Matched on age and PIQ	*Experiment 1: Prism adaptation.* Children threw balls at targets during three phases: (1) baseline phase, without wearing prism glasses (2) Adaptation phase, wearing prisms (3) post adaptation phase, without wearing prisms *Experiment 2: learning to control a novel tool.* Participants were asked to move a cursor towards a target on a computer screen, using the handle of a robotic tool. There were three phases: (1) movement trials without any perturbation (2) movement trials where either a force field was applied to the robot tool or a visual perturbation was applied so that the cursor movement rotated with respect to movement of the hand (3) post adaptation phase with no perturbation	Expt 1: Both groups showed similar levels of adaptation (reducing error during the adaptation phase) and post adaptation after effects (increased error). Expt 2: Both groups showed similar levels of adaptation (reducing error during the adaptation phase) and post adaptation after effects (increased error)	6 (learning)
Haswell et al. (2009)	*Autism:* N = 14; Age = 10.5 ± 1.7; IQ = 98 ± 20.4 *Control:* N = 13; Age = 10.4 ± 1.8; IQ = 113 ± 6.8 Unclear whether matched on age or IQ	*Learning to control a novel tool:* Children learned to control a robot arm to play a game involving catching animals that had escaped from a zoo. A force field was applied to the robot arm to build new associations between motor and sensory consequences. Intrinsic (same joint movements) and extrinsic (same target location) adaption was tested in random trials where the force field was removed	Controls showed adaptation for both intrinsic and extrinsic coordinates, whereas the autistic children showed adaptation only for intrinsic coordinates	6 (*learning*)
Mostofsky et al. (2004)	*Autism:* N = 8; Age = 8.7–13.5; IQ > 85 *Control:* N = 8; Age = 8.7–13.5; IQ > 85 Matched for age. IQ of control group significantly higher than autism group	*Ball catching:* Participants caught a ball dropped into their hand during three phases: (1) Baseline phase catching a light ball (2) adaptation phase catching a heavier ball (3) post adaptation phase catching the lighter ball again	Both groups showed similar levels of adaptation (reduction in impact displacement during phase 2) and post adaptation effects (larger initial impact displacement)	6 (learning)

Table 2 continued

Paper	Participants	Task	Findings	Motor processes tested
Barnes et al. (2008);	*Autism*: N = 14; Age = 11.6 ± 1.65; IQ = 110.4 ± 12.6 *Control*: N = 14; Age = 11 ± 1.8; IQ = 116.3 ± 13.8 Matched on age and IQ	*Serial reaction time task*: Three circles were displayed horizontally on a screen. When a circle was illuminated, participants were instructed to press a matched key. Unknown to the participants, illumination of the circles occurred in a repeated pattern, intermixed with random illuminations	Both groups showed faster reaction times to repeated then random trials, and autistic but not control children continued to show learning in the later trials (d = 0.74)	6 (learning)
Brown et al. (2010)	*Autism*: N = 26; Age = 11.5 ± 1.2; IQ = 102.4 ± 14.1 *Control*: N = 26; Age = 11.8 ± 1.6; IQ = 104.7 ± 9.4 Matched on age and IQ	*Serial reaction time task*: as above but with four locations	Both groups showed faster reaction times to repeated than random trials, particularly for later trials	6 (learning)
Nemeth et al. (2010)	*Autism*: N = 13; Age = 11.8 ± 3.4; IQ = 93.2 ± 20.7 *Control (IQ matched)*: N = 13; Age = 9.2 ± 2.6; IQ = 96.5 ± 17.7 *Control (age matched)*: N = 14; Age = 11.6 ± 3.7; IQ = 109.1 ± 12.8	*Serial reaction time task*: as above but with four locations	All groups showed faster reaction times to repeated than random trials	6 (learning)

visual stimulus using their left hand to the felt position of their unseen right arm or finger or to actively move their unseen arm to match the position of a visual stimulus. Notably, these children did show motor difficulties despite their normal proprioception. In addition, indirect evidence for intact proprioception can be derived from a study performed by Glazebrook et al. (2009). They asked autistic adults to perform a simple pointing task where vision of their hand and visual environment was either available or removed and reported that without visual feedback, the autistic participants produced equally accurate end points to neurotypical controls. However, when visual feedback was present, the autistic group exhibited relatively longer movement durations and consistently overshot the target compared to the control group. These results suggest that autistic individuals are able to successfully use proprioception and/or efference copy to guide their movement but find it harder to use visual feedback to control movement.

Several studies suggest that higher level visual processing may be atypical in autism. Thresholds for detecting coherent motion and biological motion are higher in autistic participants than typical participants, indicating difficulties in integrating sensory signals (Bertone et al. 2003; Cook et al. 2009; Freitag et al. 2008; Koldewyn et al. 2010; Milne et al. 2002, 2006; Pellicano and Gibson 2008; Pellicano et al. 2005; Tsermentseli et al. 2008). Similarly, the recognition and discrimination of faces is frequently impaired (Boucher and Lewis 1992; Klin et al. 1999). However, autistic individuals also show superior performance on tasks that place greater emphasis on lower level local detail as opposed to a more global, contextual approach such as the Embedded Figures Task (Jolliffe and Baron-Cohen 1997; Shah and Frith 1993), the Wechsler Block Design subtest (Caron et al. 2006; Shah and Frith 1993) and in visual search (Joseph et al. 2009; Kemner et al. 1998; O'Riordan and Plaisted 2001; O'Riordan et al. 2001). Researchers have proposed that this perceptual style is a result of either a reduced drive to extract overall meaning, termed *weak central coherence* (Happe and Frith 2006) or an increased dependence on local detail, termed *Enhanced Perceptual Functioning* (Mottron et al. 2006; for reviews encompassing all levels of visual function see Behrmann et al. 2006; Dakin and Frith 2005; Kaiser and Shiffrar 2009; Simmons et al. 2009). It is not yet known if weak central coherence is also found for tactile and proprioceptive information processing.

In summary, the evidence suggests that low level visual, tactile and proprioceptive inputs are intact or enhanced in autism. On the other hand, evidence from the visual domain suggests that impairments arise at the level of interpretation and integration of these signals, although additional studies are required to test whether this suggestion holds for the other senses. Hypersensitivity and an enhanced ability to detect detail in a stimulus is combined with difficulties in integrating sensory information into a coherent whole. These differences in sensory systems could contribute to motor deficits. This link between sensory input and motor control is emphasized by findings that measures of motion coherence are correlated with motor skills in autistic and neurotypical individuals (Milne et al. 2006). Furthermore, Gowen and Miall (2005) observed that performance of participants with Asperger's appeared to be worse on tasks that required greater sensory processing (e.g., pointing and timing compared to repetitive tapping and hand turning). Altered sensory input will have a direct impact on calculation of the state estimate, which is used to plan and modify movements and is discussed next.

(2) State Estimation

In order to create and update motor plans, the brain requires a state estimate of where the body is currently located as well as a sensory representation of the location, weight, speed or direction of a particular target. For example, to reach a mug of tea, you must estimate the location of the mug and the location of your own hand. Vision makes the major contribution to defining target locations, while both visual and proprioceptive/tactile information must be integrated in determining hand location. Predicted sensory inputs derived from forward models can also make an important contribution to state estimation, especially during rapid movements. The process of bringing together all these different signals is a form of multi-sensory integration (MSI).

Two core challenges can be identified in MSI. First, it is essential to determine which signals to integrate—should the cool metal of the teaspoon be integrated with the sound of the telephone or the gentle clink of stirring tea? This problem can be solved using both spatial and temporal windows, only integrating information from different senses that occurs close in *space* or *time* (Spence et al. 2004). Second, the different information sources must be weighted appropriately to make best use of the available data. For example, in daylight vision often provides the most reliable estimate of hand location, but when reaching for your alarm clock in the dark, it is better to use proprioception. Studies of typical adults demonstrate statistically optimal multisensory integration which takes into account the variability of each sensory signal (Alais and Burr 2004; Ernst and Banks 2002; Landy et al. 1995).

There are few quantitative studies examining MSI in autistic individuals at present, but it appears that integration of visual and auditory signals presented at a similar time point is comparable between ASD and

neurotypical participants (Williams et al. 2004a; van der Smagt et al. 2007). More recent studies have tested whether the usual reduction in integration found with increasing temporal separation between the visual and temporal stimuli is also present for autistic groups. Interestingly, autistic children appear to integrate visual and auditory stimuli over a larger temporal window (Foss-Feig et al. 2010; Kwakye et al. 2011) and begin to integrate these two senses at a later age than neurotypical participants (Taylor et al. 2010). In addition, the rubber hand illusion has been used to examine integration between vision, touch and proprioception (Cascio et al. 2012). In this illusion, the participant watches a rubber hand on the table in front of them, while the rubber hand and their own unseen hand beneath the table are synchronously stroked. Integration between vision and touch transfers a sense of hand ownership to the rubber hand and participants think their own hand is positioned closer to the rubber hand. Cascio et al. (2012) observed that proprioceptive drift of the participants hand towards the rubber hand occurred later in the autistic children, suggesting that proprioception is less affected by visual inputs.

No studies to date have directly examined how the different senses are weighted in ASD. With evidence for higher level sensory impairments it will be important to investigate whether sensory input is optimally weighted according to these noisy inputs. Moreover, recent studies in neurotypical participants reveal the important impact that multi-sensory weighting can have on both uni-sensory perception and motor control (Binda et al. 2007; Shams et al. 2011; Wozny and Shams 2011). For example, Binda et al. (2007) used a spatial mislocalization task where targets presented near the onset of a saccade are mislocated in the direction of the saccade due to noisy visual signals. However, the authors showed that when participants were required to localize auditory-visual targets, spatial localization during the saccade was improved due to greater weighting of the less noisy auditory signal. These findings highlight the dynamic and interdependent nature of MSI and action control as well as how inappropriate sensory weighting could lead to inaccurate and slower motor control.

(3) Motor Planning

Motor planning is the process of converting a current state (my hand is by my side) and a desired state (my hand should be on the mug) into a sequence of motor commands (move the arm, close the fingers …). In computational terms, this is an inverse problem and is solved by an inverse model. Planning often begins before a movement is initiated, but the inverse model continues to control action

and correct errors during execution. Motor planning is often considered to be hierarchical, for example, beginning with the abstract goal of making a cup of tea, it is necessary to plan the sequence of actions and then the detail of each individual movement to achieve the goal. The more abstract stages involve computing our intentions as well as using processes like memory, which help us to remember things such as which cupboard the teabags are located in. As autistic individuals are known to have impairments in executive functioning (Corbett et al. 2009; Hill 2004) we will focus on lower level aspects of planning which are more directly related to motor control.

The simplest way to assess motor planning is to study reaction times before a movement is performed, which provides a basic measure of the time taken to formulate a motor plan. Autistic participants typically show longer reaction times for reaching movements then their neurotypical counterparts (Glazebrook et al. 2006; Glazebrook et al. 2008, 2009; Mari et al. 2003; Nazarali et al. 2009; Rinehart et al. 2001; Rinehart et al. 2006a). In contrast, saccadic reaction times are similar to neurotypical comparison groups (D'Cruz et al. 2009; Goldberg et al. 2002; Luna et al. 2007; Mosconi et al. 2009; Stanley-Cary et al. 2011; Takarae et al. 2004), suggesting that planning difficulties may be more significant for limb than eye movements. In the following we discuss which aspects of the planning hierarchy appear problematic starting with the more complex and finishing with the lower level processes.

One challenge for motor planning in skilled action is the appropriate storage and deployment of motor knowledge, that is, the knowledge of how to hold and move a tool or shape the hand for a particular gesture. Impairments of skilled movements is termed dyspraxia and there is extensive evidence indicating that compared to neurotypical controls, autistic children perform worse when asked to execute a gesture (e.g., waving) and when asked to demonstrate a gesture using a tool (e.g., hammering a nail) (Dewey et al. 2007; Dowell et al. 2009; Dziuk et al. 2007; Green et al. 2002; Mostofsky et al. 2006). Even when basic motor impairments measured using test batteries are taken into account, dyspraxia is still present (Dewey et al. 2007; Dowell et al. 2009; Dziuk et al. 2007; Macneil and Mostofsky 2012). Such findings suggest the presence of specific deficits in the organization of motor knowledge involved in skilled movement performance. Those studies that report the nature of the dyspraxia reveal a number of different errors including delayed performance, altered amplitude, force or timing of the movement, incorrect limb orientation, using a body part as an object (e.g., combing hair with the hand rather than demonstrating the use of a comb) and performing an incorrect action (Dewey et al. 2007; Mostofsky et al. 2006). The example of using a body part as an object highlights that deficits may begin with higher level

motor knowledge but also extend down to lower levels of control as with incorrect limb orientation. However, the finding that autistic children can recognize object based and symbolic gestures as well as neurotypical children (Hamilton et al. 2007; Dowell et al. 2009) suggests that it is the actual transfer of motor knowledge into action that is problematic.

A second challenge in motor planning involves considering the whole of an action sequence, not just the next step. When planning grasping and placing movements, typical individuals will often pick objects up using an awkward posture in order to end in a more comfortable position (Cohen and Rosenbaum 2004; Rosenbaum et al. 1990). For example, in a grip selection task, participants are asked to pick up a bar and rotate it into a final position using either supination or pronation of the wrist. By changing the starting angle of the bar, participants are forced to choose between an awkward start, but comfortable end posture or vice versa and tend to select the former (Cohen and Rosenbaum 2004; Rosenbaum et al. 1990; Fig. 2). However, Hughes (1996) observed that a group of thirty-six autistic children were more likely to end their movement in an awkward posture, suggesting that they did not take the end position into account when planning their movements. In contrast to the above findings, van Swieten et al. (2010) found that autistic children showed equivalent sensitivity to end state comfort as age matched control children. A younger group of children as well as those with DCD were also tested with the results indicating that these groups showed a bias towards selecting a more comfortable starting grip than end position. The authors argued that the task reflects motor experience rather than predictive planning, with participants replicating the most reliable movements according to their movement ability and experience. This would suggest that the autistic children in Hughes (1996) either had less motor experience or poorer motor skills, than those in the latter studies. Hamilton et al. (2007) also tested a group of twenty-five autistic children on the grip selection task and found no group differences, further suggesting that the performance of autistic and
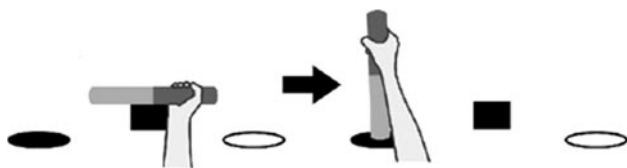

Fig. 2 Example of a version of the grip selection task. The participant's task is to put the pale end of the *bar* on the *black target circle*. This can either be accomplished by grasping the dark end in an awkward underhand grip and finishing with a more comfortable posture (shown in picture) or the participant could grasp the *bar* using a comfortable overhand grip, but finish in an uncomfortable posture. Adapted from Hamilton et al. (2007)

neurotypical children is equivalent when asked to select the appropriate sequence of task-related movements.

An alternative approach to understanding action sequencing is to consider how actions are linked together in overlapping segments, sometimes termed chunking or chaining (Berstein 1967; Gobet et al. 2001; Graybiel 1998). For example, in reaching for a piece of food, a child may begin to open his mouth to eat before even grasping the food. Thus two action components (hand movement and mouth opening) overlap in time. Some studies suggest that autistic children have difficulty in tasks involving action chaining, and are more likely to perform each action component individually. Cattaneo et al. (2007) employed electromyography (EMG) to record muscle activity related to mouth opening during a sequence of actions in eight autistic children. Participants were asked to lift an item of food and bring it to either their mouth or a container on their shoulder. During the eating task only, EMG activity in neurotypical children started before the hand even grasped the object. In contrast, EMG activity in the autistic children started much later, when the hand was bringing the food to the mouth (although Pascolo and Cattarinussi 2012 have recently failed to replicate this finding).

In a follow-up study, Fabbri-Destro et al. (2009) explored action chaining in twelve autistic children using a task where the children were required to pick up an object and place it inside either a small or large container. In the typically developing children, the initial reach to the object was slower when the final container was smaller, indicating that the difficulty of the final action goal was programmed into the entire movement sequence. In contrast, the autistic children showed no difference in movement duration between the container sizes. This could be due to a planning failure, if autistic children do not take the final goal into account when planning their actions. Alternatively, it could be a result of perceptual issues: the autistic children may have over-estimated the size of the second container so negating the requirement to adjust the speed of their initial movement.

There is also suggestion that some autistic individuals may show desynchronisation of sub-movements within a single action. Mari et al. (2003) used a reach-to-grasp task in twenty autistic children, where participants were instructed to pick up objects that varied according to size and distance. The authors found that the behaviour of their participants differed according to IQ. A lower functioning group (IQ 70–79) showed evidence of desynchonisation between the reach and grasp component, with delayed onset of the grasp component, while a higher functioning group (IQ between 80 and 109) demonstrated normal reach to grasp actions. However, this latter group produced faster movements than the control and low functioning groups suggesting that use of any visual feedback would have been minimal. These

findings raise the important issue of heterogeneity within the autism spectrum, although they contrast with the findings of Glazebrook et al. (2009) discussed earlier who found that visual feedback increased movement duration. Due to the smaller participant number (n = 13) and absence of individual IQ scores in the work by Glazebrook and colleagues, it is not possible to compare the two studies, but both highlight that the use of visual information in motor control may be problematic for autistic individuals.

Once a movement sequence has been planned, the kinematics of the actions must be determined. Fitt's law describes how movement duration is larger for smaller and more distant targets (Fitts 1954). Similarly, the timing and kinematics of reach and grasp components varies according to the size and distance of the object to be grasped: Typically, smaller and further objects result in longer movement durations, prolonged deceleration, lower amplitudes of peak velocity and decreased time of peak grip aperture. As target characteristics are taken into consideration when planning a movement (Rosenbaum et al. 2006), examining the effect of target size and distance in autistic individuals can provide information on their planning ability. Appropriate adjustments to target size and distance have been observed during pointing or grasping movements (Glazebrook et al. 2006; Fabbri-Destro et al. 2009; Mari et al. 2003), suggesting that target properties are appropriately programmed (although more slowly) for at least the immediate if not the final goal (Fabbri-Destro et al. 2009).

Prior to movement execution, movement sub-goals are planned in a hierarchical order, such as effector first, then direction and finally amplitude. Evidence for such a hierarchy comes from studies using precues where participants are given advance warning about different aspects of the upcoming movement (e.g., effector, direction, amplitude). As the effector is selected first, advance warning about which hand to use results in the largest reduction of reaction time (Rosenbaum 1980). Glazebrook et al. 2008 used a modified version of the precue technique and reported that although adult autistic participants took longer to plan their movements, they showed a similar reduction in reaction times as the control group to the different combination of precues (see also experiment 1 of Nazarali et al. 2009). Therefore, autistic individuals appear to program movement kinematics using a similar order to neurotypicals.

Overall, results on motor planning studies seem somewhat contradictory. Dyspraxia is commonly reported in autism (Dewey et al. 2007; Dowell et al. 2009; Dziuk et al. 2007; Green et al. 2002; Mostofsky et al. 2006), but knowledge of action postures is not always impaired (Hamilton et al. 2007; Dowell et al. 2009). Individuals with autism show good performance on some versions of the grip selection task (Hamilton et al. 2007; van Swieten et al. 2010) and in planning the appropriate kinematics for particular targets (Glazebrook et al. 2006; Fabbri-Destro et al. 2009; Mari et al. 2003), but poor performance on chaining tasks and a similar grip selection task (Cattaneo et al. 2007; Fabbri-Destro et al. 2009; Hughes 1996). One possibility is that task complexity and participant experience influence results across different studies. For example, dyspraxia studies use actions that are composed of several steps and have a purpose whereas studies investigating planning of movement kinematics use relatively simple and meaningless pointing tasks. An alternative possibility is that autistic individuals are able to plan individual aspects of their actions (how to grasp the bar) but are less good at organizing the temporal detail of the action in the chaining tasks. Thus, autistic individuals may plan and execute each component of the action separately and the degree to which they separate action sub-goals may depend on whether they are low or high functioning. Such a strategy is reminiscent of the autistic perceptual style described by the weak central coherence (Happe and Frith 2006) and Enhanced Perceptual Functioning theories (Mottron et al. 2006), which both emphasis that individuals with autism are good at processing details and small components but less good at integrating these into a global percept. Further study of the relationship between perceptual integration and motor integration could be used to test this possibility.

(4) Feedforward Control and Prediction

During movement execution it is essential to check if the executed action is proceeding as planned, and to correct for errors if needed. One option is to compare the sensory feedback resulting from the movement with the intended goal, termed feedback control. However, delays in sensory and motor systems make feedback control slow and unstable, especially for rapid hand movements (Miall and Wolpert 1996). To deal with these delays, the motor system uses forward models or predictors. A copy of the motor command (efference copy) is sent to a forward model, which rapidly generates a prediction of the sensory consequences of the action (Wolpert and Flanagan 2001). This sensory prediction is compared with the incoming sensory signals, so that errors can be detected rapidly.

Predictive motor control can be studied by examining rapid movement corrections before feedback would normally be available (Wolpert and Flanagan 2001). For example, when drinking your mug of tea it is critical to both grip the mug tightly (grip force) and lift upwards (load force). In a natural action, the grip force exerted by the fingers on the mug is closely synchronized with the load force of the lifting arm (Fig. 3a). However, if a passerby knocked the mug, the knock would exert a load force on
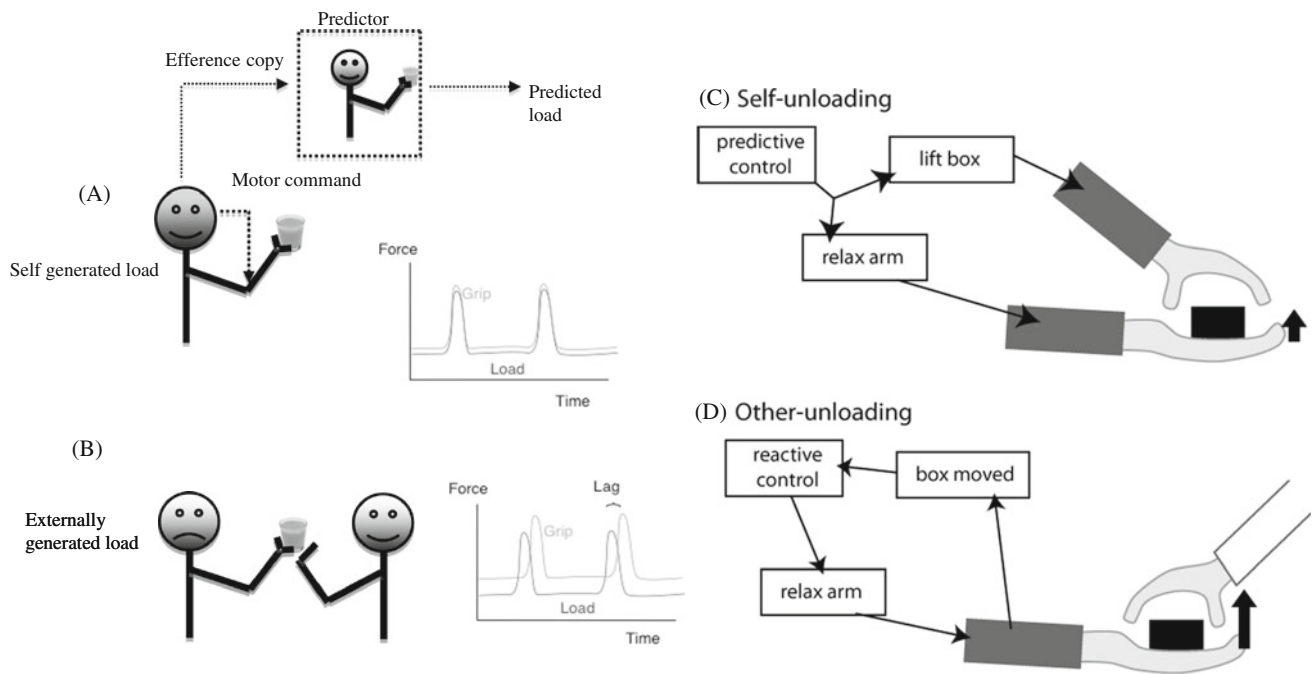
Fig. 3 In order to pick up the cup without it slipping, sufficient grip force needs to be exerted in excess of load force. When the load is self generated (lifting the cup), an efference copy of the motor command is used to predict the load force and generate enough grip force that parallels the load force (**a**). However, when the load is externally generated (another person knocks the cup), there is no prediction so grip force follows load force in a reactive manner (**b**) In the unloading paradigm, when lifting an object off your own hand (**c**), predictive control determines the time at which unloading will occur. Signals are sent to the unloading arm so that it relaxes and remains steady at the time of unloading. When another person takes an object from your hand (**d**) sensory signals are used to determine that the object has been moved. This results in reactive control with your arm relaxing following object removal and becoming less steady (adapted from Wolpert and Flanagan 2001)

the mug and you would respond around 100 ms later with a stronger grip (Fig. 3b). Thus, synchronization of grip force and load force indicates predictive control, while desynchronisation indicates reactive control (Flanagan and Wing 1997). Unloading paradigms measure the same predictive process—if you hold a heavy object on the palm of your left hand and then lift it with your right hand, predictive control allows you to keep the left hand steady (Fig. 3c). Finally, the sensory consequences of forward models can be measured in tickling and force cancellation paradigms, in which a stimulus is perceived as weaker (less tickly) when it is self-generated and thus predictable, than when it is externally generated (Blakemore et al. 2000).

Schmitz et al. (2003) used a bimanual load-lifting task where eight autistic children and neurotypical children were asked to lift a load off one hand, using their other hand while activity of their loaded arm was measured using EMG. As expected for the control children, changes in muscle activity occurred prior to unloading. However, the autistic children displayed a longer duration of voluntary unloading and reactive, rather than predictive changes in muscle activity. A potential issue with using a bimanual task is that autistic infants have been reported to display

difficulties with coordinating the two sides of the body exhibiting postural and crawling asymmetry (Esposito et al. 2009; Teitelbaum et al. 1998). Consequently, the observed reactive changes may have resulted from general deficits in bimanual coordination rather than specific problems of prediction.

As part of a wider range of tests, Gowen and Miall (2005) examined grip force control in twelve Asperger and matched control participants. Participants lifted a manipulandum up and down for ten cycles between their thumb and index finger. In the case of reduced predictive mechanisms one would expect increased latency of peak grip force in relation to peak load forced and compensatory higher grip forces. However, no significant differences were found between the groups. In contrast, David et al. (2009) observed increased latency of grip to load force in 13 autistic children and adolescents compared to a matched control sample. Blakemore et al. (2006) examined whether the sensation of tickly stimuli were attenuated in a self generated compared to externally generated condition in 16 adult ASD and 16 control participants. They observed similar attenuation of self generated tickly stimuli in both the ASD and control groups, suggesting that these partic-

ipants were able to use a sensory prediction generated by a forward model to compare with actual sensory consequences in order to attenuate the stimulation. Finally, forward models need to be adaptive in order to provide accurate predictions when changes occur to our bodies or the external environment (Shadmehr et al. 2010). Evidence reviewed later under "Motor learning" indicates that forward models involved in motor control are calibrated relatively effectively in autistic people, suggesting that the overall organization of predictive control is intact.

An alternative way to study forward models is by analogy with cerebellar patients, because the implementation of forward models is linked to the cerebellum (Blakemore et al. 2001; Kawato et al. 2003). Patients with cerebellar damage show jerky and dysmetric movements (Haggard et al. 1995), with a particular impairment in grip force-load force tasks (Hermsdorfer et al. 1994; Muller and Dichgans 1994). Individuals with autism also show slower, dysmetric movements (Glazebrook et al. 2006, 2008; Gowen and Miall 2005; Nazarali et al. 2009). However, close examination suggests these difficulties could be attributed to other motor impairments. When examining velocity and acceleration profiles of single pointing movements performed by autistic individuals, Glazebrook et al. (2006) could find no evidence of the typical discontinuities seen in cerebellar patients. However, as the autistic group performed slower movements than the control group, this could have hidden any discontinuities by optimizing the use of feedback (Beppu et al. 1984; Bastian 2006). Consequently, further data is needed on arm movement kinematics when autistic participants are required to make faster movements and where visual feedback is important.

To date, the evidence regarding the functioning of predictive control in autistic individuals appears to be mixed. Two studies using grip force and load-lifting have reported impairments in autistic children (David et al. 2009; Schmitz et al. 2003), whereas another grip force study (Gowen and Miall 2005) and one using the tickling cancellation paradigm observed no differences between adult autistic and neurotypical participants (Blakemore et al. 2006). This ambiguity could be due to heterogeneity in the groups tested, in terms of age or level of function as well as the intrinsic heterogeneity of autism. Studies with a larger sample size would help here. It is also possible that different paradigms test different aspects of predictive control. For example, in contrast to single arm grip force experiments, bimanual unloading involves inter-limb communication, which as mentioned earlier may be impaired in autism. Moreover, forward models might independently be involved in cancellation of expected sensory feedback and in online control of grasp force (Miall and Wolpert 1996). Thus, it would be informative to perform a variety of predictive experiments that have differing complexity levels and involve different movement systems within one individual.

(5) Motor Execution

Once a movement plan has been formulated, motor commands are sent to the motor cortex and on to the peripheral nerves and musculature to be executed. Errors could then arise in either the amplitude or timing of the motor signals. Variability in the amplitude of the motor signal is ubiquitous in all movement (Harris and Wolpert 1998; Jones et al. 2002), but a substantial increase in output variability would have important consequences for motor performance. For example, increased output variability could lead to errors in movement endpoint and substantial time spent on corrective movements or even task failure. Motor execution also relies on precise timing of agonist and antagonist muscle groups on a millisecond scale so that the position, orientation and speed of limbs can produce accurate movement outcomes (Hore et al. 1991, 1996). In the case of increased motor signal noise or imprecise timing one might expect dysmetric movements and increased spatial and temporal variability in certain movement parameters such as peak velocity, acceleration and duration. As highlighted earlier, dysmetria and increased end point variability is frequently reported for autistic individuals during reaching (Glazebrook et al. 2006, 2008; Gowen and Miall 2005; Nazarali et al. 2009) and saccadic movements (Luna et al. 2007; Stanley-Cary et al. 2011; Takarae et al. 2004). Increased variability of movement kinematics has also been reported. Examining pointing movements in eight autistic adults, Glazebrook et al. (2006) observed greater variability in time to peak velocity and greater spatial variability of peak acceleration which was replicated in a later study of thirteen autistic participants (Glazebrook et al. 2009). In addition, the autistic group displayed less scaling of peak velocity and acceleration when the movement amplitude increased. The authors suggested that the results indicate a problem with the generation and timing of muscular forces leading to increased variability and a strategic slowing of the movement to reduce this variability and use visual feedback (see Elliott et al. 2010 for a discussion of this study). Increased variability of stride length has also been observed in autistic but not Asperger children (Rinehart et al. 2006b; see Stanley-Cary et al. 2011 for a similar group dissociation with saccade variability) as well as increased variability of head shoulder and trunk position during walking (Vernazza-Martin et al. 2005).

Timing has been directly examined in autistic individuals using reproduction or perception tasks. In the former, participants reproduce the interval between two tones and in the latter they judge the length of one interval compared

to another so that motor demands are higher for the reproduction task. Compared to neurotypical groups, autistic performance on reproduction tasks in the range of 0.4–5.5 s consistently results in poorer accuracy and higher variability of timed responses (Gowen and Miall 2005; Martin et al. 2010; Szelag et al. 2004). These timing errors could arise from imprecision of a central clock timer or errors in a peripheral implementation system that executes the command from the clock (Wing and Kristofferson 1973). Although no previous study has differentiated between a central and peripheral timing deficit, the one study that used a perception task in children and adolescents indicated no differences between control and ASD groups (Mostofsky et al. 2000), suggesting that alterations to a peripheral implementation system as opposed to a central timekeeper may be more significant in ASD.

In summary, there is good evidence to suggest the presence of increased motor noise and timing deficits in autistic individuals and that these may lead to increased variability in temporal and spatial aspects of execution. Consequently, it may be more cognitively challenging for autistic individuals to produce accurate movements. Alternatively, increased variability could indicate deficits earlier in the model relating to planning or feedforward control, although evidence in the next section on motor learning suggests that autistic individuals can adapt and improve their movement accuracy. It will also be important for future work to determine whether timing deficits are a result of a central timekeeper or more peripheral mechanisms and how they impact upon daily motor skills.

Motor Learning

Motor adaptation is essential for enabling us to achieve motor goals when the environment and our own body dynamics are constantly changing. For example, adaptation is important in making adjustments to external properties of the environment such as the weight and location of objects to be manipulated. It also allows the motor system to make adjustments in response to changes in body dynamics such as short-term changes (e.g., muscle fatigue) as well as changes that occur over a longer timescale (e.g., developmental growth) (Shadmehr and Krakauer 2008). During adaptation, the inverse and forward models are gradually updated by comparing the actual sensory state with predictions generated by the forward model, so improving planning accuracy with successive attempts (Shadmehr et al. 2010). Adaptation paradigms generally involve an adaptation phase where participants improve their accuracy on a task where there is imposed discrepancy between motor commands and sensory feedback. This discrepancy is then removed and participants perform the

identical movement during a post adaptation phase, to test for after-effects that would indicate adaptation (or generalisation) has taken place.

Mostofsky et al. (2004) examined adaptation in eight high functioning autistic boys using a ball catching task. Participants were instructed to catch a ball dropped onto the palm of their hand and adaptation effects were measured according to impact displacement of the hand. A light ball was used in the first baseline block of trials, followed by a heavier ball during the adaptation trials with the experiment finishing with the light ball again to examine post adaptation effects. In the case of successful adaptation one would expect greater initial hand displacement with the heavier ball, reducing to a steady state displacement, followed by less hand displacement for the post-adaptation phase compared to the initial lighter ball trials. These adaptation and post adaptation effects were similar for both groups, suggesting that the autistic children in this small sample were able to adapt. Gidley Larson et al. (2008) asked autistic children to perform three tasks that required adapting to changes in the relationship between the sensory consequences of a motor output. In the prism adaptation task, children threw balls at a target before, during and after wearing prism goggles that created a shift in the visual environment. The final two tasks involved moving a cursor controlled by a robot arm to a target, where either forces were applied to the arm or the cursor was displaced in reference to the arm position. For all three tasks, the autistic children adapted their motor output to the applied perturbations and showed after effects of a similar level to the control children. Haswell et al. (2009) also observed that autistic children learnt to adapt to forces applied to a robotic arm while moving the arm to a particular location. The authors then went on to examine how well the adapted state generalised to a movement performed using intrinsic coordinates (identical joint rotations) or extrinsic coordinates (similar target location), that rely more on proprioceptive or visual signals respectively. Generalisation occurred during both conditions for the control children, but only using intrinsic coordinates for the autistic children. Moreover, generalisation was stronger for the autistic compared to control children during the intrinsic condition, suggesting that autistic children may place more weight on the proprioceptive sense when updating the forward model. These findings suggest that proprioceptive input may be more reliable than visual input and also tie in with evidence that autistic individuals are able to successfully combine proprioception with efference copy. For example, the improvement in proprioceptive precision that occurs using an active rather than passive movement task, appears similar in both adult autistic and neurotypical participants (Fuentes et al. 2011).

A different type of motor learning that appears intact in autistic people is implicit motor learning. Implicit motor

learning occurs during practice within a structured environment but where the learning is unintentional, and cannot easily be verbally described by the participant. It is commonly examined using the serial reaction time task (SRT) where participants are asked to respond to stimuli that are presented in different locations (Nissen and Bullemer 1987). Unknown to the participant, the stimuli are presented in a repetitive sequence so that the reaction times become faster for the stimuli that form part of this sequence, but participants are unable to verbally describe the repeated sequences. There is consistent evidence that the reduction in reaction times of the repeated sequences is equivalent in both ASD and neurotypical groups (Barnes et al. 2008; Brown et al. 2010; Nemeth et al. 2010). Similarly, autistic adults show unimpaired rates of learning using a predictive saccade task, where participants saccade to a target appearing repeatedly to the left then right (D'Cruz et al. 2009). However, the autistic group did show faster rightward responses, leading the authors to suggest an alteration in timing of internally generated movements, fitting with our earlier discussion on timing. Returning to arm movements, autistic participants may benefit more from practice than neurotypical participants as their overall reaction times become similar to those of the neurotypical group following practice on the repeated sequences (Brown et al. 2010). Similarly, there is some suggestion that it is possible to reduce the variability present in autistic movements through practice. Using an imitation task where participants were required to imitate simple pointing movements, we have shown that following a period of practice, variability in peak velocity of imitated movements reduced for the autistic participants to similar levels to the neurotypical group (Wild et al., unpublished data). However, it is unclear whether the benefits from practice on one task generalize to other behaviours.

In summary, there is general consensus that autistic individuals are able to successfully modify the inverse model and update a forward model prediction of arm movement when the environment changes and with repeated practice. Whether they use similar mechanisms to neurotypical individuals or rely more on proprioception during motor learning deserves further exploration.

Conclusions and Future Directions

Using a computational framework, we have reviewed different aspects of motor control in ASD and Table 2 summarizes some of the main findings. Firstly, low level sensory input seems to be the same or in some cases better in autism, while higher order sensory processing is abnormal. Secondly, it is possible that integration of these different senses is abnormal which could lead to inaccuracies in state estimation. In particular, over-reliance on proprioception could reflect either difficulties in sensori-motor integration, or an optimal response to an abnormal visual input. This requires further investigation. Thirdly, motor planning appears more challenging for autistic individuals, with difficulties in organizing motor knowledge and longer reaction times when planning movements. The evidence so far suggests that movement kinematics are planned appropriately but more slowly and that actions may not be chained together. Fourthly, evidence for the integrity of feed-forward control is mixed, indicating that further investigation is required but that predictive ability is perhaps not a key element of impaired autistic motor control. Fifthly, consistent findings of dysmetric and more variable movements suggest that increased noise and/or mistimed muscular forces may hamper movement execution. Finally, the consensus that autistic individuals show relatively intact motor adaptation indicates that basic motor learning must be intact and that flexibility exists: autistic people may have different input and output signals but the underlying "motor machinery" is functioning.

An important aspect to highlight from our review is that not all motor processes are impaired in high functioning autistic individuals and they are capable of performing a range of motor skills, but perhaps using modified processes. In particular, there is consistent evidence that motor learning is intact but that the multi-sensory inputs may be different (e.g., proprioception weighted over vision). In addition, some of the lower level planning mechanisms also appear relatively spared. In contrast, the aspects which are problematic for autistic people include sensory input and motor execution as well as higher level planning involving coordination of motor knowledge into appropriate sequences. Two non-mutually exclusive explanations can be given for this pattern of data. We consider first an explanation in terms of input/output noise, and second an explanation in terms of poor integration of information and weak central coherence.

Increased variability in both sensory inputs and motor execution are noted above. This added noise generates an additional burden at all levels of motor processing, and might make it particularly difficult to perform smooth action sequences. Planning movements in a serial fashion may represent a strategy to deal with low level noise, rather than a deficit in planning itself. Similarly, individuals might adapt to excess variability in one sensory domain by relying more on other senses. Again, apparent abnormalities in sensory integration might be an appropriate response to noisy inputs. In regards to experience and learning, as reviewed earlier there is good evidence that autistic participants are able to adapt their motor system and benefit from repeated practice of movement sequences. Perhaps

with more experience and practice, ASD individuals (particularly those who are high functioning and older) are able to overcome some of the detrimental effects of a noisy system. Such a possibility could be related to the tendency to perform repetitive behaviours: repeating an action leads to improved reaction times whereas a new action may result in a slower and less accurate outcome.

To test this input/output noise hypothesis, it would be helpful to examine sensory and motor variability in more detail in autism using methods which dissociate noise generated through sensory or execution processes (Osborne et al. 2005; van Beers 2007). Such paradigms could be used to assess whether practice reduces sensory or motor noise and how this affects motor ability. Furthermore, a useful future approach would be to explore the relationship between sensory noise and the weighting of vision, proprioception and touch and what impact this has on motor ability.

A second possible account of motor difficulties in autism focuses on the integration of motor information. Multisensory information must be brought together in state estimation, and motor knowledge must be integrated for effective planning over many timescales. A processing style focused on detail, as found for sensory systems (Happe and Frith 2006) might also have critical consequences for motor systems. In particular, impaired MSI might lead to noisier state estimates. Poor motor knowledge might lead to dyspraxia and difficulties in tool use and action knowledge tasks. Therefore, weak central coherence may extend across multiple systems in autistic individuals. To test this hypothesis, it would be helpful to know if weak central coherence in purely perceptual tasks correlates with performance on motor planning and multisensory integration tasks.

In conclusion, our review suggests that altered sensory input and variability in motor execution, together with deficits in organizing motor knowledge may play an important role in the motor abilities of autistic people. Future research should examine the precise role of sensorimotor noise in autistic motor performance and the link between weak central coherence and motor planning. An improved understanding of motor systems in autism also raises important questions for future research such as whether the underlying motor difficulties in autism and DCD overlap. Furthermore, it has been suggested that we can use our own motor processes to predict and understand the behaviour of others (Wolpert et al. 2003). This possibility raises the question of how motor difficulties relate to social difficulties—are they independent or do underlying motor issues cause the social characteristics? Using a computational approach to understanding autistic motor control may provide some insight into these questions.

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