Special issue: Review

What can autism teach us about the role of sensorimotor systems in higher cognition? New clues from studies on language, action semantics, and abstract emotional concept processing

Rachel L. Moseley [a,b,c,*] *and Friedemann Pulvermüller* [b,d,e,f]

[a] Department of Psychology, Bournemouth University, Poole, UK
[b] Medical Research Council Cognition and Brain Sciences Unit, Cambridge, UK
[c] Autism Research Centre, University of Cambridge, Cambridge, UK
[d] Brain Language Laboratory, Department of Philosophy and Humanities, WE4, Freie Universität Berlin, Berlin, Germany
[e] Berlin School of Mind and Brain, Humboldt Universität zu Berlin, Berlin, Germany
[f] Einstein Center for Neuroscience, Berlin, Germany

ARTICLE INFO

ABSTRACT

Within the neurocognitive literature there is much debate about the role of the motor system in language, social communication and conceptual processing. We suggest, here, that autism spectrum conditions (ASC) may afford an excellent test case for investigating and evaluating contemporary neurocognitive models, most notably a neurobiological theory of action perception integration where widely-distributed cell assemblies linking neurons in action and perceptual brain regions act as the building blocks of many higher cognitive functions. We review a literature of functional motor abnormalities in ASC, following this with discussion of their neural correlates and aberrancies in language development, explaining how these might arise with reference to the typical formation of cell assemblies linking action and perceptual brain regions. This model gives rise to clear hypotheses regarding language comprehension, and we highlight a recent set of studies reporting differences in brain activation and behaviour in the processing of action-related and abstract-emotional concepts in individuals with ASC. At the neuroanatomical level, we discuss structural differences in long-distance frontotemporal and frontoparietal connections in ASC, such as would compromise information transfer between sensory and motor regions. This neurobiological model of action perception integration may shed light on the cognitive and social-interactive symptoms of ASC, building on and extending earlier proposals linking autistic symptomatology to motor disorder and dysfunction in action perception integration. Further investigating the contribution of motor dysfunction

* *Corresponding author.* Bournemouth University, Poole House, Fern Barrow, Poole, BH12 5BB, UK.
   E-mail address: rmoseley@bournemouth.ac.uk (R.L. Moseley).

1.   Can autism shed light on the role of sensorimotor systems in higher cognition?

In many purely cognitive accounts, the roles of perception, emotion and especially movement are considered secondary to mental activities. But … [mental activities] are founded in emotion, perception, and action … even small difficulties with these processes early in life can have lifelong consequences." (Thelen, 2005, p. 262).

A preponderance of behavioural, neuropsychological and neuroscientific literature has challenged the traditional boundaries between 'higher-order' language and thought and 'lower-order' movement and sensory input; has countered the notion of combinatorial, logical manipulation of amodal symbols as the primary means of cognition (Anderson, 2003; Fodor & Pylyshyn, 1988; Machery, 2007); has demonstrated, instead, that neural substrates for thought, language and movement are intrinsically interwoven and functionally interdependent. In this framework, known as 'embodied' or 'grounded' cognition,[1] conceptual thought and retrieval of meaning involves the complete or partial reactivation, in a simulative manner, of neural sensorimotor activation experienced during initial concept acquisition (Allport, 1985; Barsalou, 1999, 2008, 2010; Gallese & Lakoff, 2005; Lakoff, 1987; Lakoff & Johnson, 1980; Langacker, 1987; Pulvermüller, 1999).

With a particular focus on action cognition, empirical neuroscience has demonstrated that sounds, spoken and written words with action-related meaning produce somato-topic semantic activation of the human motor system (in particular motor and premotor cortex) across multiple experimental contexts (Aziz-Zadeh & Damasio, 2008; Grisoni, Dreyer, & Pulvermüller, 2016; Grisoni, McCormick-Miller, & Pulvermüller, 2017; Hauk, Johnsrude, & Pulvermüller, 2004; Hauk, Shtyrov, & Pulvermüller, 2008; Kana, Blum, Ladden, & Ver Hoef, 2012; Pulvermüller, Shtyrov, & Ilmoniemi, 2005; Shtyrov, Butorina, Nikolaeva, & Stroganova, 2014; Shtyrov, Hauk, & Pulvermüller, 2004; Tettamanti et al., 2005). Neural control of movement includes a cascade of cortical areas (primary motor, premotor and supplementary motor cortex, located in precentral gyrus and adjacent sulci [BA 4 and BA 6]) and subcortical regions (such as the striatum and the putamen) along with the cerebellum, most of which have been seen to be activated by words with action affordances (Carota, Moseley, & Pulvermüller, 2012). The above studies highlight the involvement of *cortical* motor regions (primary motor, premotor and supplementary motor cortex) in action semantics, and so our review henceforth focuses on these areas as the 'motor system'.

There is strong evidence to suggest that activity in these regions indexes semantic processing rather than reflecting post-comprehension thought processes. First, although task conditions may suppress it, motor system activation whilst processing action-related stimuli is manifest even if participants do not actively attend to language input (Grisoni et al., 2016; Moseley, Pulvermüller, & Shtyrov, 2013; Pulvermüller, Shtyrov, et al., 2005; Shtyrov et al., 2004, 2014; Trumpp, Traub, & Kiefer, 2013; Trumpp, Traub, Pulvermüller, & Kiefer, 2014). Second, motor activation during processing of action language is flexible, following the pattern expected for semantic mechanisms (for discussion, see Pulvermüller, 2013). In particular, a flexible pattern of semantic priming has been revealed in the sensorimotor cortex (Grisoni et al., 2016). Third, frontocentral activity emerges in the semantic learning of novel action words (Fargier et al., 2012; James & Swain, 2011; Kiefer, Sim, Liebich, Hauk, & Tanaka, 2007; Liuzzi et al., 2010). Fourth, overt movement or stimulation of these motor areas has a causal effect on simultaneous processing of specific types of action words. Vice versa, action word processing may impact on specific motor mechanisms, with effects visible in behaviour and in electrophysiological brain recordings[2] (Amoruso et al., 2013; Fischer & Zwaan, 2008; Glenberg & Kaschak, 2003; Ibanez et al., 2012; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Rueschemeyer, Lindemann, van Elk, & Bekkering, 2009; Schomers & Pulvermüller, 2016; Schomers, Kirilina, Weigand, Bajbouj, & Pulvermüller, 2015; Shebani & Pulvermüller, 2013). Fifth, and finally, movement disorders and clinical impairments to motor systems are associated with specific processing impairments or abnormalities for action-related words which call on action knowledge in the retrieval of their meaning (Bak & Chandran, 2012; Boulenger et al., 2008; Cardona et al., 2014; Cotelli et al., 2006; García & Ibáñez, 2014; Grossman et al., 2008;

---

[1] These terms are often used interchangeably, but, as 'embodied cognition' situates simulation in bodily experience, it may exclude the situation of concepts in the physical and social environment which is also experienced through the senses (Barsalou, 2010). Barsalou suggests that 'grounded cognition' "captures the broad scope of grounding mechanisms, while not placing undue emphasis on the body" (2010, p. 721), and so this is the preferred terminology in this work, though 'embodiment' or 'embodied' will be used in the same sense when used by other authors in this way.

[2] We note that more fundamental *perception* of word phonology, alongside semantics, is also influenced by modulation of the motor systems, and refer the interested reader to the recent reviews by Skipper, Devlin, and Lametti (2017) and Schomers and Pulvermüller (2016).

Kemmerer, 2015; Neininger & Pulvermüller, 2001, 2003; Pulvermüller et al., 2010).[3]

Whilst the effects of motor damage on action word processing have been thoroughly documented in many populations with acquired brain damage or disease states, we here examine grounded cognition and action semantics through the lens of a very different type of movement disorder. Autism spectrum conditions (ASC)[4] are neurodevelopmental syndromes characterised by impairments in social interaction, communication and language, and, furthermore, by repetitive behaviours and intense, rigid interests. These lifelong conditions are typically diagnosed in toddlerhood or childhood in the Western world (Christensen et al., 2016; Lord & Spence, 2006) and are strongly heritable (Robinson et al., 2016; Vorstman et al., 2017; de la Torre-Ubieta, Won, Stein & Geschwind, 2016). ASC are markedly heterogenous in presentation, spanning the 'classic' cases which may or may not be accompanied by intellectual disability (Kanner, 1943) to highly verbal individuals with Asperger Syndrome (AS) (Asperger, 1944). Since both are subsumed under 'autism spectrum disorder' in DSM-5 (American Psychiatric Association, 2013), we likewise use ASC, 'autism' or 'autistic' to refer to both autism *and* AS. In standard text books, the autistic triad of deficits in social interaction, communication, and social imagination (the third criterion is alternatively named as repetitive and restricted behaviour and interests; Wing, Gould, & Gillberg, 2011) are typically highlighted. Motor deficits and any influence they might have on higher cognition have been largely overlooked, with the exception of a few authors whose work we explore in this paper. We attempt to build on this previous work with a neurobiological perspective on ASC which emphasises a possible deviance in action perception integration.

The causal aetiology of ASC is debated, so this syndrome complex presents a challenge unlike the well-defined and more precisely localised diseases of prior action word studies, such as focal stroke (Kemmerer, Rudrauf, Manzel, & Tranel, 2012), Parkinson's disease (Boulenger et al., 2008) and motor neurone disease/amytrophic lateral sclerosis (Bak & Chandran, 2012; Grossman et al., 2008). Nevertheless, we suggest that the study of autism affords a broader perspective on the grounding of cognitive processes in sensorimotor systems. It may open new perspectives on the role of the cortical motor systems in action and language understanding, and

even in other forms of quite abstract higher cognition and social processing. The autistic phenotype is "an emergent property of developmental interactions between many brain regions and functions" (Belmonte et al., 2004, p. 646), and so affords an opportunity for more critical consideration of the experience-dependent nature of conceptual representations (Casasanto, 2011; Hauk & Pulvermüller, 2011; Tschentscher, Hauk, Fischer, & Pulvermüller, 2012; Willems, Peelen, & Hagoort, 2010). Below we explore the perspective that it may be a case of the typical developmental trajectory gone awry, a case where early motor disruption, evinced in behavioural studies reported below and in frontotemporal dysconnectivity (Catani et al., 2016; Moseley et al., 2016; Roberts et al., 2014), may ripple and derail multiple domains where autistic symptomatology consequently emerges.

Here, we begin by reviewing the motor deficits of autism, their pervasiveness across the spectrum (related to age, sex and different ASC diagnoses), and their specificity to ASC. We move from the reviewed behavioural evidence to discuss the underlying neural abnormalities in cortical motor systems and recent evidence about the neuroanatomy of ASC, especially concerning atypical long-distance corticocortical links (Section 3). The general involvement of motor systems in language development and their more specific contribution to semantic learning will be used to (tentatively) explain, in part, the early relationships between autistic movement and language impairments (Section 4). In Section 5, we spell out a grounded neurobiological theory viewing action perception integration as a basic mechanism for language and cognition, explaining how information mixing and associative learning may give rise to a role for motor systems in representing action semantics. This section raises the hypothesis that motor impairments will be related to disordered semantic processing of types of words which rely on the foundational integrity of motor systems; ASC afford us a strong test case to examine the functional importance of motor systems for semantic processing, and so the hypotheses raised in Section 5 are reinstated and examined in Section 6. Section 7 describes experiments which further support and expand these hypotheses. Moving away from a specific focus on language and semantic processing, we then consider the potential significance of motor impairments and action perception integration deficits for the wider symptomatology of neurodevelopmental conditions (Section 8), touching on the wider role of sensorimotor systems in aspects of higher cognition, such as social and pragmatic communication, action prediction, and theory of mind (ToM). Finally, highlighting parallels with and additions to previously suggested models of ASC, we suggest pathways for further investigation that might, eventually, open important avenues for intervention (Section 9).

---

[3] Although we speak here of the role of motor systems in understanding action semantics, of further note is a more general role for motor areas for language understanding, which has been shown by a number of recent studies and reviews (Murakami, Kell, Restle, Ugawa, & Ziemann, 2015; Möttönen, Dutton, & Watkins, 2013; Schomers & Pulvermüller, 2016; Skipper et al., 2017; Smalle, Rogers, & Möttönen, 2015).

[4] The term 'autism spectrum disorder' (ASD) is commonly used in the literature and is synonymous with our use of ASC, but we prefer the latter term which was devised to be less value-laden, to reflect autism as a different cognitive style as opposed to an illness (see Baron-Cohen, 2000, for extensive discussion). Terminology used to speak of autism is a divisive and emotive issue (see Kenny et al., 2016; Sinclair, 2013), as is the removal of Asperger syndrome from DSM-5 (Giles, 2014; Kite, Gullifer, & Tyson, 2013). Since opinion is divided, we use both person-first and identity-first language in this paper.

2. Movement disorder in autism: a review

"His movements never unfolded naturally and spontaneously — and therefore pleasingly — from the proper coordination of the motor system as a whole." (Asperger, 1944, p. 57).

In his original case studies (1944), Asperger commented on the unusual clumsiness of his patients. Kanner (1943) paid less

attention to their motoric condition, but his report does mention the 'good motor coordination' (p. 232) of one child and another that 'had always appeared awkward in her motility' (p. 229). Whilst clinical cases studies such as these paint rich portrayals of the autistic syndrome, empirical investigation of motor disorder has, of course, been necessary to examine whether motor impairment occurs more often in autism than might be expected by chance alone. Fortunately, there is a rich literature in this area: a Pub Med search for 'autism movement' yielded 112 results, whereas 'autism motor' yielded 361 results. In our review of behavioural findings in this area, our focus is on *studies comparing motor development, motor performance or motor milestones between autistic individuals and control groups, or between individuals within the autism spectrum*. Whilst studies without comparison controls groups have obvious limitations, we include them for the sake of the descriptive data they provide. Consequently, we exclude a) studies not written in English; b) animal studies; c) single case studies; d) studies which do not report behavioural findings (for example, Dawson, Warrenburg, and Fuller (1983), which focuses on lateralization of brain activity but not performance; e) studies focussing on interventions; f) studies focussing on motor *stereotypies* as consistent with repetitive and restricted behaviours and interests, and g) studies which, by 'abnormal motor behaviour', actually investigate physical, so-called 'problem' behaviours (externalizing, 'acting out', rule breaking: e.g., Efstratopoulou, Janssen, & Simons, 2012). In terms of sample, we exclude studies whose sample focuses on a) children or adults described as having 'mental retardation' or being 'sub-normal' or 'psychotic' (prior to 1975), who cannot therefore be confidently identified as autistic; b) children or adults described merely as having 'learning disabilities' or as being 'savants', for the same reason; c) siblings of autistic individuals (a group we discuss further below); and d) children or adults with another developmental disorder, such as attention-deficit/hyperactivity disorder (ADHD) or Fragile X syndrome, with comorbid autism or autistic traits. As previously mentioned, movement control involves a complex coordination of brain regions and of course, involvement of prefrontal cortex. Much has been written about prefrontal cortex and executive function in autism, and so whilst the coordinated control of behaviour obviously contributes to controlled movement, we did not include studies whose primary focus was on executive functioning, inhibition and sequencing of movements rather than motor performance per se (e.g., Hughes (1996)). We did, however, include studies specifically examining the earliest stages of motor preparation/planning which attempt to tease apart motor versus executive planning[5] and motor deficits in execution (e.g., Rinehart, Bradshaw,

Brereton, & Tonge, 2001; van Swieten et al., 2010). Likewise, we included studies of perceptual-motor integration where they emerged in our search and involved tasks assessing motor performance, as this is also an important aspect of motor proficiency. We exclude studies investigating broader aspects of action cognition, such as those investigating differences in *perception of movement* and movement *observation* (for which there is a wide literature). Whilst we did not search for them, we include studies concerning imitation and gesture where they emerged in our search and are associated with motor tasks (e.g., Stone, Ousley, & Littleford, 1997) in so far as despite their social component, impaired reproduction of gestures may reflect motor disorder as well as social and/or symbolic-conceptual deficits. Where studies do examine other domains as well as motor function, these are summarized very briefly.

The results of our literature search in their entirety are displayed in Supplementary Materials, and we summarise here the major questions they purport to answer. The answer as to whether motor dysfunction occurs in autism is self-evident: we reviewed 92 studies. However, **does motor dysfunction in autism occur more often than might be expected to occur by chance in a typical population?** Precisely 49 studies comparing ASC and typically-developing (TD) control groups answer this question in the affirmative. The more methodologically rigorous studies, those which a) either matched for chronological and/or mental age and/or IQ *or* b) controlled for these in their analyses, *and* c) had more sizeable groups (>30 per group) demonstrate that motor impairments occur more often than might be expected in TD children (Abu-Dahab, Skidmore, Holm, Rogers, & Minshew, 2013; Ament et al., 2015; Dewey, Cantell, & Crawford, 2007; Dowell, Mahone, & Mostofsky, 2009; Duffield et al., 2013; Dziuk et al., 2007; Floris et al., 2016; Sumner, Leonard, & Hill, 2016; Travers et al., 2015, 2016). A meta-analysis of 41 studies confirmed that, despite substantial variation, effect sizes are large with TD participants significantly outperforming individuals with autism in motor coordination, arm movements, gait and postural stability (Fournier, Hass, Naik, Lodha, & Cauraugh, 2010), and that these effects did not seem affected by publication bias.

The question naturally follows as to **what *kind* of motor deficits are reported?** Many studies addressed this question with movement assessment batteries with normative percentiles for performance and objective scoring: for example, the PANESS (Dowell et al., 2009; Dziuk et al., 2007; Floris et al., 2016; Jansiewicz et al., 2006; Mostofsky, Burgess, & Gidley Larson, 2007), the M-ABC or M-ABC2 (Ament et al., 2015; Green, Baird et al., 2002; Green, Moore, & Reilly, 2002; Green et al., 2009; Hanaie et al., 2013; Hanaie et al., 2014; Kopp, Beckung, & Gillberg, 2010; McPhillips, Finlay, Bejerot, & Hanley, 2014; Miyahara et al., 1997; Sumner et al., 2016; Whyatt & Craig, 2012), or the Bruininks-Oseretsky test (Dewey et al., 2007; Ghaziuddin & Butler, 1998; Hilton, Zhang, Whilte, Klohr, & Constantino, 2012; Pan, 2014). These measures yield total scores which were sometimes analysed alone, but they each assess a range of fine and gross motor skills, including balance and gait, hopping or jumping, repetitive sequential movements of the hands and feet, manual dexterity and ball skills (catching and throwing). Alongside poorer total performance, the subscale differences

---

[5] This distinction is explained by the latter authors as one where executive planning involves sequencing choices or moves in order to achieve a desired end goal state, thus requiring abstract thoughts about the goal state (often playing through the first few moves in one's imagination) and placing demands on working memory. Motor planning (or preparation), in contrast, is described as being based on learnt movement skills and not relying on working memory (van Swieten et al., 2010), and involves chaining the most basic kinematic aspects of movement to complete a motor act (Fabbri-Destro, Cattaneo, Boria, & Rizzolatti, 2009).

particularly highlighted by these studies are in slower repetitive movements; overflow; gait; balance; dysrhythmia; manual dexterity and coordination; and ball skills. Some of these (overflow, gait, balance and speed of timed movements) are indeed predictive of ASC diagnosis (Jansiewicz et al., 2006). Not all studies using motor batteries report deficits (Hauck & Dewey, 2001; Miller, Chukoskie, Zinni, Townsend, & Trauner, 2014), but notably, both of these used less refined and fine-grained measures.

Different methodologies have corroborated motor battery deficits and reported others in addition. Ball skills, most notably in catching a ball, are highlighted by numerous reports (Ament et al., 2015; Green et al., 2009, Green, Baird et al., 2002; Green, Moore, & Reilly, 2002; Hanaie et al., 2013; Papadopoulos et al., 2012; Staples & Reid, 2010; Whyatt & Craig, 2012). More fine-depth analysis of gait, for example using electronic walkways (Rinehart, Tonge, Bradshaw et al., 2006; Rinehart, Tonge, Iansek et al., 2006) or infrared cameras and sensors placed on the body (Nobile et al., 2011), corroborate the difficulty that movement batteries report in heel-to-toe walking, and further report gait irregularities (for example greater variance in stride length and velocity), ataxia, reduced range of motion in the joints, and difficulty walking in a straight line. Abnormalities in postural stability have been documented using an electronic balance board (Nintendo Wii), which showed that autistic participants had more difficulty maintaining balance (Travers, Powell, Klinger, & Klinger, 2013). Discriminant analysis has shown that autistic children can be sensitively and specifically classified according to the speed, force and pressure of their finger movements on a tablet screen (Anzulewicz, Sobota, & Delafield-Butt, 2016); machine learning was also seen to correctly identify them by the kinematics of reach-to-drop (Crippa et al., 2015) and reach-to-throw tasks (Perego, Forti, Crippa, Valli, & Reni, 2009). Other studies of kinematics in very basic arm movements and reaching and grasping reveal differences between autistic and TD participants (Campione, Piazza, Villa, & Molteni, 2016; Cook, Blakemore, & Press, 2013). Use of more traditional neuropsychological tests reflect poorer performance in the grip strength (Abu-Dahab et al., 2013; Hardan et al., 2003; Travers et al., 2015, 2016), finger tapping (Abu-Dahab et al., 2013; Duffield et al., 2013; Hardan et al., 2003; Travers et al., 2016) and pegboard tasks (Abu-Dahab et al., 2013; Ament et al., 2015; Barbeau, Meilleur, Zeffiro, & Mottron, 2015; Duffield et al., 2013; Hardan et al., 2003). These tests ascend in difficulty, primarily testing muscle strength, simple motor coordination and dexterity respectively.

Several studies have reported on motor milestones, either through home-video analysis (Baranek, 1999; Gernsbacher, Sauer, Geye, Schweigert, & Hill Goldsmith, 2008; Ozonoff et al., 2008; Teitelbaum, Teitelbaum, Nye, Fryman, & Maurer, 1998) and/or interviewing parents (Gernsbacher et al., 2008; Kopp et al., 2010; Lloyd, MacDonald, & Lord, 2013; Ozonoff et al., 2008; Sumner et al., 2016). These studies are methodologically problematic in the respect that video rating is open to human error (though most studies blind raters to diagnosis), videos cover a small and selective snapshot of early life, and retrospective reports are open to inaccuracy. This may partly explain some of the variance in these findings. Sumner et al.'s (2016) parent sample did not report a delay in crawling,

standing and walking between TD and autistic infants. Nor did Lloyd et al.'s (2013) analysis of the few items concerning motor milestones in the ADI-R (Le Couteur, Lord, & Rutter, 2003). Gernsbacher et al.'s (2008) parental reports suggest a delay in crawling and in numerous oral-motor milestones such as blowing kisses; Ozonoff et al.'s (2008) parental reports reflect significant delays in walking and trends towards delays in crawling and sitting. This study differentiated between autistic children with and without early regression. They found that parental reports for infants without regression did not differ significantly from TD infants, but the authors applied a second analysis where growth curves between two time points were modelled from video recordings, parental reports, and movement battery assessments. Interestingly, the autistic children without regression were significantly older when they showed their most mature level of motor control whilst lying prone or supine, whereas the autistic group with regression only differed in their growth curve in the later-developing milestone of walking, leading the authors to suggest "an active pathological process" disrupting motor domains (p. 12). Other reports of the earliest emerging autistic symptoms, although they do not specify whether they discuss autism with or without regression, do indeed note motor dysfunction within the first 12 months (Guinchat et al., 2012; Young, Brewer, & Pattison, 2003).[6] Aside from milestones, abnormalities in lying (Esposito, Venuti, Maestro, & Muratori, 2009) have been reported in autistic infants, as have unusual posturing (Baranek, 1999) and differences or reductions in general spontaneous movement (Phagava et al., 2008; Zappella et al., 2015). Abnormalities in the writhing, fidgety movements that typically emerge in early life are symptomatic of minor or major neurological deficits (Einspieler et al., 2014).

Although we did not include them in our own review, we also perused extant reviews and short communications on the topic of autistic motor dysfunction (Bhat, Landa, & Galloway, 2011; Casartelli, Molteni, & Ronconi, 2016; Cook, 2016; Downey & Rapport, 2012; Esposito & Paşca, 2013; Gowen & Hamilton, 2013; Matson, Matson, & Beighley, 2011; McCleery, Elliott, Sampanis, & Stefanidou, 2013; Miyahara, 2013; Parma & de Marchena, 2015; Rinehart & McGinley, 2010) and note several more studies which did not emerge in our own search due to their describing very specific abnormalities. These speak of deficits such as in handwriting (Kushki, Chau, & Anagnostou, 2011) and (relatedly) fine-precision grip (David, Baranek, Wiesen, Miao, & Thorpe, 2012); in postural stability (Molloy, Dietrich, & Bhattacharya, 2003) and as documented in the studies above, gait (Esposito & Venuti, 2008; Vernazza-Martin et al., 2005; Vilensky, Damasio, & Maurer, 1981); of akinesia, dyskinesia and bradykinesia (Damasio & Maurer,

---

[6] Motor symptoms are not the only symptoms that appear in the first year of life; we refer the interested reader to several other papers which point out early abnormalities in social orientation among other symptoms in the first year of life (Clifford & Dissanayake, 2008; Clifford et al., 2013; Clifford, Young, & Williamson, 2007; Dawson et al., 2004; Maestro, Muratori, Barbieri et al., 2001; Maestro, Muratori, Cavallaro et al., 2001; Osterling, Dawson, & Munson, 2002; Ozonoff et al., 2010; Saint-Georges et al., 2010; Zwaigenbaum et al., 2005).

1978; Maurer & Damasio, 1982); and finally of hand dystonia and facial grimacing (Wing, 1981).

Additionally, although we did not search for them specifically we did include in our review studies comparing imitation in TD and ASC participants, despite the probable contribution of social impairments to this ability. Poorer imitation, pantomiming and reproduction of meaningful and meaningless gestures (with or without tools) in autism is ubiquitous across studies (Biscaldi et al., 2014; Cossu et al., 2012; Dewey et al., 2007; Dowell et al., 2009; Dziuk et al., 2007; Green, Baird et al., 2002; Green, Moore et al., 2002), although notably this study did not possess appropriate norms for comparison; Miller et al., 2014; Stone et al., 1997; Vanvuchelen, Roeyers, & De Weerdt, 2007), especially when they involve simultaneous movements (McAuliffe, Pillai, Tiedemann, Mostofsky, & Ewen, 2017). The ability to perform skilled motor gestures (such as brushing your teeth, using a tool) is known as *praxis*, with dyspraxia being the inability to perform such learnt skilled movements. Deficits in gesture and imitation, whether these are of transitive (with an imaginary or real object), intransitive (without an object, e.g., waving) or meaningless gestures, are predictive of autistic symptoms and whilst related to motor skills, remains predictive of diagnosis once motor performance is factored out (Dowell et al., 2009; Dziuk et al., 2007; Miller et al., 2014). It is interesting, however, to consider the most common types of errors that autistic people make: needing more attempts, only partially replicating actions, showing abnormal synkinesias (unintentional movements of other parts of the body in parallel), using part of the body as an object, orientating the hand incorrectly, or misjudging the amplitude, force or size of gestures. Whilst imitation and gestural deficits do not appear to be solely attributed to motor dysfunction, Vanvuchelen et al. (2007) note that these are all *spatial* errors, which they and others (Rothi & Heilman, 1997) link to deficits in the 'action production system' rather than problems with recognition and representing actions and gestures. The need for more attempts is linked by these same authors to motor planning and execution deficits.

Indeed, several researchers have queried whether the motor deficit in ASC is related to the actual execution of the movement or, instead, to the preparation/planning/programming of movements. Experimental paradigms designed to test this typically measure and discriminate between planning time (for example, the time taken between seeing a visual cue and initiating a movement) and execution time (the time between initiating a movement and terminating it) (Dowd, McGinley, Taffe, & Rinehart, 2012; Nazarali, Glazebrook, & Elliott, 2009; Rinehart, Bellgrove, et al., 2006; Rinehart et al., 2001; Stoit, Schie, Slaats-Willemse, & Buitelaar, 2013). Other tasks have also added an element of reprogramming, where participants must divert from an expected movement (Rinehart et al., 2001), or added levels of complexity (such as inhibition) to try tease apart motor and executive planning (Rinehart, Bellgrove, et al., 2006). Some paradigms have required participants to grip an object wherein selecting the easiest initial movement may lead to an uncomfortable end-point (van Swieten et al., 2010). Some studies reveal slower or impaired motor planning (Mari, Castiello, Marks, Marraffa, & Prior, 2003; Rinehart, Bellgrove,

et al., 2006), but others do not (Stoit et al., 2013; van Swieten et al., 2010); a later study showed that movement preparation time was not significantly longer in ASC but significantly more *variable* (Dowd et al., 2012), which may explain (along with the small sample sizes in several of these studies) why it is sometimes observed and sometimes not. Other studies show difficulties reprogramming planned movements (Nazarali et al., 2009; Rinehart et al., 2001). Some reveal only execution deficits (Stoit et al., 2013), which these authors linked to impairments in the internal feedforward models guiding movement; some reveal weaknesses in planning *and* execution (Mari et al., 2003; Nazarali et al., 2009). The interesting *lack* of effect caused by a visual distractor, in ASC, was suggested by the authors to reflect that people with ASC do not generate alternative or multiple motor plans for potential actions (Dowd et al., 2012). This is interestingly related to another task framed around the ability of people with ASC to perceive affordances (the type of grip to use on an object, the size of an aperture their hand could fit through) and adjust their movements online, a task which arguably also requires motor planning and revealed difficulties in the autistic group in judging and executing the movements (Linkenauger, Lerner, Ramenzoni, & Proffitt, 2012). A similar line of enquiry related to motor planning concerns whether motor preparation, in people with ASC, reflects anticipation of expected actions, with several studies suggesting that this is indeed an area of impairment (Brisson, Warreyn, Serres, Foussier, & Adrien-Louis, 2012; Rinehart et al., 2001; Schmitz, Martineau, Barthélémy, & Assaiante, 2003; Stoit et al., 2013).

We shall return to the type of motor deficits seen and their putative neural substrates in the next section, but the second critical question to address concerns the ubiquity of motor problems; **are they prevalent throughout the spectrum, in individuals of any age, sex or specific ASC diagnosis?**

Many studies have compared participants with high-functioning autism (HFA) and those with AS. A risk with these studies is that the validity of their findings relies on initial, accurate categorization of participants; the lack of differentiation between AS and HFA, in the case of Manjiviona and Prior (1995), is likely to reflect invalid categorization based on the diagnostic manuals of the time. Some studies find greater motor deficits in individuals with HFA than those with AS (Behere, Shahani, Noggle, & Dean, 2012; Ghaziuddin & Butler, 1998; Green et al., 2009; Papadopoulos et al., 2012; Rinehart, Bellgrove, et al., 2006), others find the opposite picture (Iwanaga, Kawasaki, & Tsuchida, 2000), some find deficits of different types in both groups (Rinehart et al., 2001), and some find no statistical difference between groups (Jansiewicz et al., 2006; Noterdaeme, Mildenberger, Minow, & Amorosa, 2002). Some of these studies have very small samples (Behere et al., 2012; Ghaziuddin & Butler, 1998; Iwanaga et al., 2000; Rinehart, Bellgrove, et al., 2006; Rinehart et al., 2001), casting doubt on their findings. Furthermore, some studies also add in a third comparison with individuals with Pervasive Developmental Disorder Not Otherwise Specified (PDD-NOS: a form of 'atypical autism' that was ever nebulous), adding more uncertain, inconsistent results to the pool (Ghaziuddin & Butler, 1998). The lack of clear, consistent distinction between any of these groups may reflect the contention around subtyping among clinicians and researchers. Indeed, this

controversy has led to the dissolution of AS (and indeed PDD-NOS) in DSM-V (American Psychiatric Association, 2013), and more recent studies involve groups of individuals with *an autism spectrum condition*. This practice suggests it may be more prudent to look instead for differences related to language development, autistic regression, or IQ (/mental age). IQ is strongly related to motor skills, with lower IQ associated with poorer performance across a range of measures (Barbeau et al., 2015; Dewey et al., 2007; Dowell et al., 2009; Dziuk et al., 2007; Ghaziuddin & Butler, 1998; Green et al., 2009; Hilton et al., 2012; Kopp et al., 2010); unsurprisingly, where studies classify participants as having low functioning autism (or low IQ), they unanimously perform worse than those with HFA or AS (or autistic participants with high IQ) in many motor tasks (Papadopoulos et al., 2012; Paquet, Olliac, Bouvard, Golse, & Vaivre-Douret, 2016; Vanvuchelen et al., 2007). Failing to match groups of HFA and AS individuals on IQ casts further doubt on supposed differences between them (Ghaziuddin & Butler, 1998), and on the findings of studies which do not control for IQ between groups or consider it in their analysis (problematically, this is not always reported). Language problems are of course often related to IQ and so naturally, autistic individuals with better current and/or historic language skills tend to perform superiorly in most motor tasks (Barbeau et al., 2015; Belmonte et al., 2013; Gernsbacher et al., 2008; Hsu et al., 2004; McPhillips et al., 2014): as we shall go on to discuss, language requires motor proficiency and so this is hardly surprising. Finally, a single study previously mentioned investigated motor differences between autistic children with and without developmental regression, finding different patterns of motor impairment which may reflect different pathological processes (Ozonoff et al., 2008). This study only concerned infants, and so the later differences between these groups would be of interest.

Indeed, when considering the ubiquity of movement deficits in autism, it is important to ascertain **when these become evident, and whether they persist throughout life.** Since autism is rarely diagnosed before a child is a toddler and often later, investigating the first years of life in autistic children often relies on parental memories or retrospective analysis of videos, both problematic methods (Palomo, Belinchón, & Ozonoff, 2006; Saint-Georges et al., 2010). Whilst some studies claim that signs of autistic movement dysfunction are present in the first 4–6 months of age and provide rich descriptive data (Teitelbaum et al., 1998), they lack strong scientific grounding. A more rigorous alternative lies in the study of infant siblings of an autistic individual ("baby sibs"), who, at increased risk of being diagnosed with ASC themselves, can be closely monitored from birth (Newschaffer et al., 2012). We conducted a second, smaller review of these studies, the terms and results of which can be found in Supplementary Materials. Many of these studies assess performance at several time-points. Some suggest that motor differences can be seen as early as 6 months in high-risk (HR) infants, more so than would be expected by chance (Flanagan, Landa, Bhat, & Bauman, 2012; Iverson & Wozniak, 2007; Nickel, Thatcher, Keller, Wozniak, & Iverson, 2013), but others find fine and gross movement to be developing normally at 6 months and to derail later at 12–14 (Landa & Garrett-Mayer, 2006; Ozonoff et al., 2014) or 18–24 months

(Landa, Gross, Stuart, & Bauman, 2012); some studies only scrutinise a later period and find motor deficits at that point (e.g., 12 months: Mulligan & White, 2012). Notably, significant differences may only appear at a certain point following a slow deviance off the developmental trajectory. Landa, Gross, Stuart, and Faherty (2013), for example, found that the widening divergence in fine motor skills between HR-autistic and non-autistic groups only reached significance at 36 months. Some studies do not detect movement deficits at all (Zwaigenbaum et al., 2005: these authors use an insensitive measure which does interestingly reveal motor deficits in another baby sibs study [Brian et al., 2008]), whereas some studies find differences in one motor battery but not another (Toth, Dawson, Meltzoff, Greenson, & Fein, 2007). Studies which investigate parental concerns corroborate the variation in findings: where some report that parents of infants who are later diagnosed as autistic express significantly more concerns about movement problems from 6 to 24 months than do parents of HR-TD infants (Sacrey et al., 2015), others classify motor skills among more general concerns (e.g., eating and sleeping problems) and in comparison with specific social autistic symptoms, find them less discriminatory between groups (Ozonoff et al., 2009). Lebarton and Iverson (2013) found parents to report significant manual and oral motor delays at 12 and 18 months in HR compared with LR infants, but again reported substantial variation between infants.

Parental reports may introduce variability through their inherent subjectivity, but there may be several other reasons for the inconsistency seen across studies. For one, not all studies consider IQ as a covariate. Secondly, there is a great deal of variation in the eventual outcome and cognitive and motor trajectories of HR infants (Landa & Garrett-Mayer, 2006; Landa et al., 2012, 2013). Most obviously, some will be diagnosed autistic and others not, so collapsing them within one group may result in differences being missed. Several studies have found that when the HR infants are further stratified by their eventual outcome, those later to be diagnosed as autistic are significantly likely to show the pattern of poor motor trajectories (Landa et al., 2012) or to differ on motor performance at set time-points from HR-non-autistic infants (Brian et al., 2008; Landa & Garrett-Mayer, 2006; Lebarton & Iverson, 2013; Nickel et al., 2013; Sacrey et al., 2015). As most of these studies involve infants, the range of motor deficits investigated is much smaller and less information is available for the type of motor impairments shown. These studies do, however, reveal that in some HR infants later diagnosed with autism, motor deficits are evident within the first 15 months of life, whereas other autistic infants within the same group have a slower derailing of motor abilities (Landa et al., 2012, 2013).

Despite this degree of inconsistency, these studies suggest that motor dysfunction appears to be present from very early life in autism. Does it, however, **persist to adulthood?** Where adults are studied, they are often grouped with adolescents in samples with substantial age range [Hardan, Kilpatrick, Keshavan, & Minshew (2003), for example, include an autistic group with an average age of 19 but who range from 8 to 43 years old] — a period in which neuroanatomy is likely to undergo gross alterations. Such wide-ranging samples are unlikely to capture *particular* characteristics of adolescents or adults, but nevertheless suggest that motor deficits exist in

older populations (Barbeau et al., 2015; Biscaldi et al., 2014; Cook et al., 2013; Linkenauger et al., 2012; Sachse et al., 2013; Thompson et al., 2017; Travers et al., 2016, 2013). Where studies investigate age as a continuous variable affecting motor performance, such as with longitudinal designs, they suggest that the deviance in motor performance may widen with age (Lloyd et al., 2013; Travers et al., 2016) – this certainly requires further investigation. Anecdotal reports from autistic adults describe motor impairments with significant impact on wellbeing and functionality (Robledo, Donnellan, & Strandt-Conroy, 2012). This, and the relationship between motor function and functional daily living skills (Jasmin et al., 2009; Macdonald, Lord, & Ulrich, 2013; Travers et al., 2016), suggest that ameliorating motor dysfunction in ASC is worthy of considerable attention. We shall go on to explore the full ramifications of motor disorder in the remainder of this paper.

The last question regarding the ubiquity of motor deficits within the autism spectrum concerns **whether they occur regardless of sex**. The vast majority of studies include male samples; a single study confirms the presence of motor dysfunction in a small female group (Kopp et al., 2010). We included the study in our review as some interesting results emerged, such as the association between motor dysfunction and autistic symptomatology but not between motor dysfunction and ADHD. The methodology is otherwise problematic, however, involving an extraordinary number of measures and thus comparisons. Moreover, 95% of the small autistic sample had comorbid ADHD and 35% had learning disabilities, so the nature of motor dysfunction in autistic females and how they might compare with males is yet to be ascertained. A lack of consideration of sex differences may also contribute to the variation seen in baby sibs studies, given that several early social and attentional symptoms thought to predict autistic symptomatology in HR infants are only predictive in males (Bedford et al., 2016).

The next important question is the specificity of motor impairment: **are motor problems *specific* to ASC, or extant to a similar extent in other populations with developmental disorders?** Most common targets for comparison are developmental coordination disorder (DCD), ADHD, and specific language impairment (SLI). Problematically, these studies often involve fairly small groups who may have overlapping comorbidities, do not control for IQ, and may involve multiple comparisons that are uncontrolled for. If we first consider ADHD, the multiple comparison problem is true for Dewey et al. (2007), who report significantly better motor (and imitation) skills in children with ADHD, but fortunately not for Mostofsky et al. (2007) or for Ament et al. (2015), who both report significantly better motor performance in ADHD (most notably for balance and catching a ball in the Ament study). Another study reporting better motor skills in ADHD is stymied by lack of IQ matching (Pan, Tsai, & Chu, 2009). Kopp et al.'s (2010) findings are, as previously mentioned, confounded by comorbid diagnoses and the multiple comparison problem. Van Waelvelde et al. (2010) find no differences between autistic children and those judged to be 'at risk' of ADHD. Interestingly, Hilton et al. (2012) found better performance in participants with ASC and ADHD than those with ASC alone. Again, we are uncertain if multiple comparisons were controlled for, but this would seem consistent with

an admittedly small sampled study which found that children with ADHD but without comorbid autism do not differ in movement skills from TD children (Papadopoulos et al., 2012). One consideration pertinent to discussion, here, is whether participants were taking medication, which is not always reported or controlled for (e.g., Ament et al., 2015; Dewey et al., 2007) and which is known to affect variables such as gait (Jansiewicz et al., 2006).

Only one study investigated SLI: McPhillips et al. (2014) found no significant difference in total motor skills, with the only difference being in one of the manual dexterity tasks where autistic children were significantly poorer at threading laces. This study apparently failed to control for multiple comparisons, but as this could result in false positives, the lack of difference in total motor score and subtests seems to reflect a genuine lack of difference in this group. In consideration of DCD, there is again inconsistency: some report poorer motor skills and later milestones in DCD (Sumner et al., 2016) and worse motor planning (though lacking IQ measures [van Swieten et al., 2010]), whereas others report poorer performance in autism (Dewey et al., 2007). Problematically, not all studies test whether autistic children themselves meet criteria for DCD (as apparently many of them do [Green, Baird et al., 2002; Green, Moore et al., 2002; Kopp et al., 2010; Hilton et al., 2012]).

Methodological weaknesses such as those mentioned above may account for some of the variance in findings. Further problematically, subtypes have been proposed to exist in DCD (Lalanne, Falissard, Golse, & Vaivre-Douret, 2012; Vaivre-Douret et al., 2011), SLI (Friedmann & Novogrodsky, 2008; Naama Friedmann & Novogrodsky, 2011) and ADHD (Fair et al., 2012). As such, the motor profiles of these different conditions are yet to be fully ascertained (especially as all these studies have involved child samples), but the answer as to the specificity of motor disorder to autism would therefore at present have to be negative. If motor systems do play a role in higher cognitive function, the presence of motor deficits in developmental conditions such as SLI (Hill, 2001; Marton, 2009; McPhillips et al., 2014; Ullman & Pierpont, 2005; Zelaznik & Goffman, 2010), and the presence of higher cognitive deficits in conditions such as DCD (Asonitou, Koutsouki, Kourtessis, & Charitou, 2012; Dewey, Kaplan, Crawford, & Wilson, 2002; Wilson & McKenzie, 1998), is unsurprising. In the above paragraphs, we begin to observe, for example in the studies of movement planning, that movement disorder can result from disruption at one or several stages in the cognitive and underlying neural chain of movement production. Movement difficulties, in ASC as in any clinical population, motivate investigation of the neural substrates for gross and fine movement, and we now move to discuss the well-documented neural substrates of movement disorder in ASC and, below, the very specific predictions that these studies allow us to make about higher cognitive function.

3. The neuroanatomical correlates of movement impairment

Motor deficits in ASC indicate several likely neural culprits, the first being the cortical motor system (primary motor [M1],

premotor and supplementary motor cortex). Within primary motor cortex, increased grey matter volume and surface area in the right motor cortex (trending towards significance in the left) set autistic children apart from TD children and those with ADHD (Mahajan, Dirlikov, Crocetti, & Mostofsky, 2015). An excess in white matter in M1 has also been reported in autistic children and correlated with movement impairment (Mostofsky et al., 2007), leading these authors to suggest that stronger local connectivity in motor cortex indicated by radiate white matter volume might come at the cost of impaired long-distance connections of motor systems. The relationship between anatomical connectivity and *functional* connectivity, the correlated brain activity which is understood to reflect communication within and between brain networks (Fox & Raichle, 2007), is far from transparent, but functional connectivity is constrained by the biological architecture of the brain (Honey et al., 2009). Accordingly, it is unsurprising that differences in functional connectivity occur: that during a movement task (finger tapping), synchronized activity between left and right M1 and between M1 and other motor regions (cerebellum, thalamus and supplementary motor cortex) was seen to be reduced in children with ASC (Mostofsky et al., 2009). Whilst participants were at rest, another study documented abnormal lateralization characterized by functional hyper-connectivity in right M1 and hypoconnectivity in left M1, and a relationship between this rightwards shift and poorer gait, total PANESS scores and speed of timed movements (Floris et al., 2016). Abnormal lateralization and especial hyperconnectivity of right M1 was also reported by Carper, Solders, Treiber, Fishman, and Müller (2015).

The motor cortex is functionally parcellated into regions corresponding to the control of different body parts: a motor homunculus, with representation of the feet and legs at the most dorsal and lateral point of precentral gyrus, representation of the hands and arms inferior to this on the medial aspect of precentral gyrus, and most ventrally, representation of the face, mouth and tongue. (Postcentral gyrus, adjacent to this, contains a similar sensory homunculus processing information from each of these regions). Nebel, Joel et al., 2014 examined the functional parcellation of M1 in ASC and found reductions in functional segregation between the upper and lower limbs; abnormalities were also seen in the region linked with dexterous, complex movements of hand, arm and shoulder. The authors suggest that functional organization of M1 was immature in their child participants (a conclusion also posited by Carper et al. (2015), who interpret functional hyperconnectivity in the motor system to reflect reduced functional segregation). Thompson et al. (2017) examined the structural integrity of the short fibres connecting the local homuncular regions of M1 and adjacent postcentral gyrus (somatosensory cortex) in a wide-ranging age group of adults with ASC (18–45 years old). They found abnormalities in the connections between the motor and sensory hand regions which was associated with poorer performance in the pegboard test. Interestingly, the differences in correlations between control and autistic groups suggested a lack of the typical left dominance for motor performance in the autistic group, and that this reduced asymmetry was related to poorer performance, as also found by Floris et al. (2016).

The majority of the findings above purport to children, and it is important to note that age may strongly modulate neural connectivity. Functional connectivity, at least, seems to trend from hyperactivity in childhood towards normalization or hypoactivity in older age (Dajani & Uddin, 2016; Nomi & Uddin, 2015). Anatomically, the *increased* grey matter seen in primary motor cortex by Mahajan et al. in autistic children is contradicted by a relationship between reduced grey matter and poorer finger-tapping in autistic adults (Duffield et al., 2013). Sex may also be an important modulator of brain structure and function, but as in the previous section, autistic girls and women are grossly understudied. Preliminary findings suggest that white matter volume in left supplementary motor area and left M1 can reliably discriminate between autistic girls and boys (Supekar & Menon, 2015), so whether the androcentric findings above hold true for females is yet to be ascertained.

We have seen, above, that autistic individuals also show deficits in broader aspects of action-related cognition, including imitation and gesturing. Imitation deficits in particular have been described in terms of impairments in 'self-other mapping' (Williams, 2008; Williams, Whiten, Suddendorf, & Perrett, 2001): the ability to connect an observed action with the motor program necessary to perform a similar movement oneself, possibly with a similar goal. The mechanism of this perception-to-action mapping has been posited in mirror neurons, a type of sensorimotor neuron[7] responsive both when a specific action is carried out and when the same action type is perceived visually or acoustically (Rizzolatti & Sinigaglia, 2010). Neural activity attributable to mirror neurons in premotor and motor cortex is abnormally low in ASC (Bernier, Dawson, Webb, & Murias, 2007; Cattaneo et al., 2007; Dapretto et al., 2006; Honaga et al., 2010; McCleery et al., 2013; Nishitani, Avikainen, & Hari, 2004; Oberman et al., 2005; Rizzolatti & Fabbri-Destro, 2010; Théoret et al., 2005; Wadsworth et al., 2017),[8] and therefore was interpreted as support for proposals that the autistic phenotype results from the dysfunction of mirror neuron systems (the 'broken mirrors' hypothesis: Ramachandran & Oberman, 2006).

The success of this hypothesis depends on the envisaged (and theory-dependent) role of mirror neurons in socio-communicative processes including action and intention understanding. Rizzolatti and colleagues purport that a range of neurons in frontoparietal regions are responsive to different levels of action understanding. These include coding basic

---

[7] Mirror neurons are one type of cell within the motor system (in contrast to canonical motor cells without multimodal properties, i.e., not responsive to action perception); they have been found in primary motor cortex (Fadiga, Craighero, & Olivier, 2005), premotor cortex (Grèzes, Armony, Rowe, & Passingham, 2003; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), supplementary motor cortex (Mukamel et al., 2010), and posterior inferior frontal gyrus (Kilner, Neal, Weiskopf, Friston, & Frith, 2009), which is sometimes considered part of the motor system. They have also been found in inferior parietal cortex (Rizzolatti & Sinigaglia, 2010), parahippocampal gyrus and entorhinal cortex (Molenberghs et al., 2012; Mukamel et al., 2010).

[8] Autism is conceptualized as a spectrum which merges seamlessly into the typical population. It is interesting thus that autistic traits alone have been suggested by some authors to modulate MNS activity (Puzzo, Cooper, Vetter, Russo, & Fitzgerald, 2009).

transitive actions directed towards goal objects; coding different types of grip that would support different intentions (grasp to eat *vs* grasp to place [Cattaneo et al., 2007]); coding the expressive manner in which actions are conducted (Di Cesare, Di Dio, Marchi, & Rizzolatti, 2015); and coding chains of simple actions that could represent more complex intentions (Giese & Rizzolatti, 2015; Rizzolatti & Fabbri-Destro, 2010; Rizzolatti & Sinigaglia, 2010). In contrast, Hamilton (2016) envisions the mirror system as under top-down control by a higher-order region and thus modulated in its response by features such as familiarity and social context. In this view, the mirror system is believed to respond to the rather rudimentary basic kinematics or goal of an action, with the more complex intentional understanding of action assigned to a higher-order region, tentatively named as the medial prefrontal cortex, which controls activation of the mirror neuron system (see also Wang & Hamilton, 2012). Likewise, Hickok (2014) stipulates that, while mirror systems activate during typical observation of actions, entirely different regions in posterior temporal cortex provide the 'gateway to understanding'. In this view, motor mirror regions play a mostly epiphenomenal role, possibly that of action selection, linking perceived actions with appropriate responses in the individual's motor repertoire (for a more extensive discussion, see Schomers & Pulvermüller, 2016). How these named regions interact and the precise role of each in action understanding remains debated (see, for example, Garagnani, Wennekers, & Pulvermüller, 2008; Giese & Rizzolatti, 2015; Westermann & Miranda, 2004), as does their involvement in the symptomatology of ASC, and the arguments for each position demand a review all of their own. Indubitably, because the human homologues of areas where mirror neurons are typically found in monkeys are not globally unresponsive across all circumstances in ASC (see, for e.g., Becchio & Castiello, 2012; Enticott et al., 2013; Oberman, Ramachandran, & Pineda, 2008), it has however been rightly noted that claims about mirror neurons being simplistically and universally 'broken' in ASC are problematic (Hamilton, 2013). However, the suggestion that these cells behave in an atypical manner in ASC appears consistent with the literature. In Sections 4 and 5, we shall go on to suggest more specific mechanisms interlinking perception and motor information, which may be necessary for integrating action with perception knowledge and, likewise, for 'building' mirror neurons and the sensorimotor circuits they are likely embedded in (Pulvermüller, Moseley, Egorova, Shebani, & Boulenger, 2014). As relates to autism, we suggest it preferable to speak about deficits in action-perception mapping, rather than solely ascribing these mapping problems to one single type of neuron. We will return to this discussion below.

Shifting our attention to wider motor circuits of the brain, a large body of research reviewed by Bo, Lee, Colbert, and Shen (2016) suggests that people with ASC may exhibit a deficit in motor learning: the ability to fluidly adapt movement in response to sensory/motor input ('motor adaption') and to combine isolated movements into smooth, coherent sequences. Deficits in motor adaption implicate the cerebellum, where cell abnormalities in the cerebellar vermis and hemispheres are a robust feature of ASC (Fatemi et al., 2012; Rogers et al., 2013). Several studies suggest that children with ASC rely on proprioceptive feedback for motor adaptation and are impaired when learning motor skills through visual input alone (Izawa et al., 2012; Mostofsky & Ewen, 2011; Sharer, Mostofsky, Pascual-Leone, & Oberman, 2015; Vanvuchelen et al., 2007; Wild, Poliakoff, Jerrison, & Gowen, 2012). Hyposensitivity and hypersensitivity to visual and proprioceptive feedback respectively is indeed correlated with abnormalities in the anterior, sensorimotor aspect of the cerebellum in children with ASC (Marko et al., 2015). The cerebellum has also been linked to gait dysfunction in ASC (Nayate, Bradshaw, & Rinehart, 2005; Rinehart, Tonge, Iansek, et al., 2006). In a small sample, Hanaie et al. (2013) documented abnormalities in the cerebellum, in autistic children, which predicted poorer motor skills and poorer ball skills (these authors did not measure gait). Travers et al. (2015) found cerebellar abnormalities to predict tapping speed in autistic children and adolescents. As previously noted, functional communication between the cerebellum and the rest of the motor system was reported to be compromised (Mostofsky et al., 2009).

Autistic deficits in motor preparation (Rinehart, Bellgrove, et al., 2006; Rinehart et al., 2001), call into question the integrity of frontostriatal motor loops, which are indeed structurally and functionally atypical in ASC (Chukoskie, Townsend, & Westerfield, 2013; Di Martino et al., 2011; Langen et al., 2009; Takarae, Minshew, Luna, & Sweeney, 2007). Specific examination of the structural integrity of basal ganglia and their relationship to motor performance in grip strength, finger tapping and pegboard performance failed to reveal a correlation or abnormalities in a large group of autistic individuals between 8 and 45 years of age (Hardan et al., 2003). The lack of difference or relationship in this study might potentially reflect the within-group brain development in such a wide-ranging sample: structural differences of the basal ganglia were associated with poorer motor skills and praxis in autistic children (Qiu, Adler, Crocetti, Miller, & Mostofsky, 2010). Motor planning deficits were also theoretically linked to deficits in the ability of anterior cingulate to regulate attention for actions and to impaired communication between cingulate and supplementary motor cortex to the difficulty initiating motor programmes (Rinehart et al., 2001). Abnormal movement-related potentials, which are associated with preparation of internally-generated movements and linked to the chain of basal ganglia, thalamic and supplementary motor communication, have indeed been reported in HFA (Enticott, Bradshaw, Iansek, Tonge, & Rinehart, 2009). Interestingly the small AS group (n = 12) in this study did not differ from controls, to whom they were IQ-matched, and it is unclear if IQ (non-matched between HFA and TD groups) was controlled for in the significant different in movement-related potentials.

Abnormalities in the organization of and communication between cortical neural networks are implied by a range of reports on atypical structural and functional connectivity in ASC (Casanova & Trippe, 2009; Courchesne & Pierce, 2005; Di Martino et al., 2014; Ecker et al., 2010; Geschwind & Levitt, 2007; Moseley, Shtyrov et al., 2015; Moseley, Ypma et al., 2015; Nomi & Uddin, 2015; Vissers, Cohen, & Geurts, 2012; Ypma et al., 2016).[9] These are supplemented by theoretical

---

[9] Again, like mirror neuron activity, functional connectivity appears to be modulated by autistic traits alone (Barttfeld et al., 2013).

accounts of ASC in terms of brain-wide dysfunction characterized by 'noisy' or dysfunctional neural communication (Belmonte et al., 2004; Minshew & Goldstein, 1998; Rubenstein & Merzenich, 2003). In autistic children and adolescents, Travers et al. (2015) indeed found reduced structural integrity of the long-ranging corticospinal tract of fibres which arise from motor cortex and travel to the brainstem; this related to poorer grip strength and finger tapping, and to autistic symptomatology. Hanaie et al. (2016) also found correlations with poorer motor performance and reduced integrity in parts of the brainstem which connect to the somatosensory cortex through the thalamus, which connect the cerebellum to the brainstem, and the superior longitudinal fasciculus connecting the supramarginal gyrus and inferior parietal sulcus with frontal motor systems.

The cognitive effects of disruption in corticocortical communication would be felt at many levels. It is notable at this point to speak of visuomotor or action-perception integration, a component of skilled, coordinated movements archetypally displayed in the hand-eye coordination required to catch or hit a ball with a bat or even in the climbing of stairs (Linkenauger et al., 2012). In the laboratory, it often contributes to tasks such as those of executive function which require fast pointing towards a target as it appears (Sachse et al., 2013). Deficits in action-perception integration would explain particular difficulties in estimating movements with reference to the size and orientation of objects and spaces (Linkenauger et al., 2012), and why complex tasks involving sequential actions, speed and accuracy are especially difficult for autistic participants (Miller et al., 2014; Whyatt & Craig, 2012). Action-perception integration would also explain why visual stimuli are suggested to not prime motor programmes as they do in TD controls (Dowd et al., 2012). Catching a ball is highlighted as an especial deficit in ASC (Ament et al., 2015; Green, Baird et al., 2002; Green, Moore et al., 2002; Hanaie et al., 2013; Papadopoulos et al., 2012; Staples & Reid, 2010; Whyatt & Craig, 2012), and is linked by several of these authors to deficits in what Whyatt and Craig (2012) describe as "perception-action coupling". Furthermore, although we did not extend our review to broader aspects of motor cognition such as movement perception, communication between motor and perceptual systems also appears to be integral for effective perception of biological motion (Cook et al., 2013; van Kemenade, Muggleton, Walsh, & Saygin, 2012) and abnormalities of biological motion perception are robustly documented in autism (Cook et al., 2016; Freitag et al., 2008; Koldewyn, Whitney, & Rivera, 2011). At brain level, action-perception integration is especially dependent on the integrity of corticocortical connectivity, and functional connectivity between posterior, basic visual areas (BA 17/V1, BA 18/V2), higher-order visual processing areas in extrastriate cortex and precentral and postcentral gyri has indeed been observed to be reduced in autistic children, most especially between upper limb regions and higher-order visual areas (Nebel et al., 2016). This reduction was related to more severe social impairments.

As previously mentioned and demonstrated in this section, motor deficits can result from a break-down in one or multiple processes and their underlying neural substrates. It is highly likely that the motor deficits seen in the different developmental conditions, which may not always be distinguishable

behaviourally, have differing neural origins, hence the different symptom complexes in these conditions. The neural substrates of motor dysfunction in DCD, ADHD and SLI have not received quite as much attention: there are many hypotheses regarding DCD but few with neurobiological support from brain imaging (see reviews by Brown-Lum & Zwicker, 2015, and Gomez & Sirigu, 2015: of these, the corpus callosum, cerebellum, parietal lobe and basal ganglia are highlighted, but studies contain extremely small samples); studies of SLI have mainly focused on perisylvian language cortices (see Mayes, Reilly, & Morgan, 2015 for review, but note that these authors admit the confusion regarding classification of this condition across studies). ADHD and autism are commonly comorbid, both more commonly diagnosed in males[10] and seem to both be characterized by abnormal connectivity (Kern et al., 2015; Konrad & Eickhoff, 2010); they may be set apart by the concentration of dysconnectivity in particular regions. We are not however aware of studies focussing on the neural substrates of motor dysfunction and connectivity related to movement in ADHD, presumably as this is a less salient feature of this condition.

As there is a preponderance of documentation regarding the motor deficits in autism and their putative neural substrates, we therefore focus on ASC in this review, although motor disorder can and does appear in other developmental disorders. We return to consider these in our final remarks, but focus in the main on the documented neural substrates for motor disorder in autism, most particularly the strong case that has been made for dysconnectivity within motor systems and between motor systems and other cortical regions, which allow us to make specific hypotheses concerning the effects this dysconnectivity might have on higher cognition. Most notably, with the deficits of action-perception integration discussed above, we return in Section 6 to findings of dysconnectivity in ASC pertinent to action-perception linkage in language, notably those facilitating communication between motor systems and other cortical regions. Before we can consider the full ramifications of action-perception disruption, we must first however discuss the typical linkage of language and motor systems, which we proceed to do in Sections 4 and 5.

4. Language and motor development in typical and autistic infanthood

"… motor development is not an independent process, but has rich and complex relationships with the development of other cognitive domains …" (Leonard & Hill, 2014, p. 167).

To understand the broad impact of early motor impairment in autism and other childhood conditions marked by

---

[10] A genuine difference in the prevalence of autism and ADHD in males and females could offer vital aetiological clues (see for example (Lai, Lombardo, Auyeung, Chakrabarti, & Baron-Cohen, 2015), for discussion of genetic mechanisms), but is heavily debated; the imbalance may reflect that these conditions are less commonly *diagnosed* rather than less prevalent (again, see Lai et al., 2015).

movement deficits, it is necessary to draw back and consider the typical role of motor systems in language and cognitive development. The body is the brain's vehicle for world exploration; small wonder that cognitive development climbs steeply with motor development in infancy (Lenneberg, 1967). In early life, an infant's range of speech sounds is constrained by their early oral motor skills, particularly their ability to control and coordinate movements of the jaw, lips and tongue (Green, Baird et al., 2002; Green, Moore et al., 2002; Nip, Green, & Marx, 2009). As the speed and breadth of orofacial movements increases, spontaneous soundless movements become replaced by cooing (from ~3 months of age), babbling (~6 months), and then by first words (~12 months), which form the majority of orofacial movements by the end of the second year (Nip et al., 2009). The later ability to sit inflates lung capacity and improves control over subglottal pressure, such that sitting is followed by a cascade of phonological and articulatory development (Yingling, 1981, cited in Iverson, 2010), including the production of consonant-vowel articulations.

The basic motoric activity of babbling has long been seen as a precursor of language development. However, in light of neurobiological theory, babbling may serve an important function of building cortical circuits (Locke, 1993) which are later reused for repetition, recombination and innovative use of language elements (Pulvermüller et al., 2014). Note that the production of syllables, as it dominates the stage of repetitive babbling, implies the activation not only of neurons in frontal articulatory motor areas (where speech output is controlled) but at the same time of auditory neurons in posterior temporal areas responding to the self-produced sounds; similar co-occurrence of activity is present in somatosensory fields in anterior parietal cortex. Such babbling-related co-occurrence of neuronal activity has been shown (by computer model simulations [Garagnani et al., 2008; Garagnani, Wennekers, & Pulvermüller, 2009]) to yield circuits that interlink motor and sensory neurons. Because they interlink information about actions and their related perceptions, we call these circuits 'action perception circuits'. Likewise, manual babbling may give rise to action perception circuits for hand movements, which are later reused in gesturing and other cognitive activity. If action perception circuits serve a central role in building language and social-communication mechanisms, any abnormalities in the connectivity between frontal and temporal lobes must impact on language and on action understanding more generally. Elementary social interaction that normally emerges in the later part of the first year after the phase of oral and manual babbling, such as repeating others' hand gestures and words, would in particular require functional sensorimotor links.

Further to social interaction and development, the progression of gross motor skills such as shuffling, crawling, standing and walking, radically alters an infant's relationship with the objects and people around him or her and provides a wealth of new learning experiences (Iverson, 2010). Previously unseen or unreachable objects are now visible and can potentially be manipulated, opening new interactions with others (Karasik, Tamis-Lemonda, & Adolph, 2011). The breadth of adult vocal feedback rockets as infants become mobile; adults remark on their behaviour and furthermore vary the affective content of their speech when infants encounter risky scenarios (Clearfield, 2011; Karasik, Tamis-Lemonda, & Adolph, 2014).

Increased control of the hands affords gestural communication, which many believe to be a key precursor to language development (Iverson & Goldin-Meadow, 2005; Liszkowski, 2008). The development of rhythmic arm movements, i.e., shaking a rattle, slightly precedes or coincides with vocal babbling (Bates & Dick, 2002; Iverson, Hall, Nickel, & Wozniak, 2007; Locke, Bekken, Mcminnlarson, & Wein, 1995), and is suggested to afford infants the ability to practice the skills underlying rhythmic, timed vocalisations and to receive multimodal feedback on their actions (Iverson, 2010; Iverson & Thelen, 1999; Thelen, 1995). Certain hand and head gestures are predictive of language comprehension and vocabulary in young children (Cochet & Byrne, 2016; Hsu & Iyer, 2016; Özçalışkan, Adamson, & Dimitrova, 2015), as are facets of social development like joint attention (simplistically, the ability to understand pointing gestures, manifest in looking to where a finger points, rather than at the pointing finger; to share the attentional focus of another person through being directed via non-verbal [eye-gaze, pointing] or verbal means). Joint attention, in turn, also relies on motor development (Campos et al., 2000), and is strongly linked to learning word-object relationships (Baldwin, 1995). It has been posited that children with gross motor deficits may have fewer resources for the development of joint attention (Mody et al., 2017). Ultimately, development of social and cognitive domains cannot be separated from co-occurring development of motor (and sensory) systems, which are dynamically interwoven (Thelen & Smith, 1994).

With this in consideration and with regards to the early motoric dysfunction reported above, it is unsurprising that language delays and abnormalities are an essential aspect of diagnostic criteria for autism[11] (Eigsti, De Marchena, Schuh, & Kelley, 2011; Lord, Risi, & Pickles, 2004; Luyster, Kadlec, Carter, & Tager-Flusberg, 2008); after all, sound production is a motor act which requires considerable control. First words are almost universally delayed in autistic children (Howlin (2003) puts the delay at on average 38 months), and babbling and first vocalisations are significantly reduced at ages 9—12, 15—18 and 16—36 months (Patten et al., 2014; Plumb & Wetherby, 2013; Schoen, Paul, & Chawarska, 2011; Warren et al., 2010). Given the importance of early vocalisations for building sensorimotor links, this may offer some explanation for the early language and babbling deficits of ASC; although, notably,

---

[11] Though we do recognise changes to nosology: DSM-IV (APA, 2000) had a three-factor model specifying impairments in the domains of 'social interaction', 'communication' (involving language criteria) and restricted and repetitive behaviours and interests, but DSM-5 combines the first two factors into a single factor called 'social communication'. The two-factor model better fits the symptom presentation of people with autism (Frazier et al., 2012; Mandy, Charman, & Skuse, 2012). This downplaying of language symptoms implies that these are no longer an essential aspect of diagnosis, but in fact, gold-standard diagnostic tools, the ADOS-G (Lord et al., 2000) and the ADI-R (Le Couteur et al., 2003), have not been yet adapted to the new DSM criteria and so language abnormalities (such as pronoun reversal and many more) remain central to diagnosis.

a more primal sensory-motor integration deficit could also result in less sensory activity transmitted to frontal motor systems and consequently less babbling. Regardless of the direction of the relationship, studies have indeed shown that movement impairment in ASC is predictive of language development. The ability to imitate motor acts, which includes the ability to repeat verbal utterances, at two years of age, was seen to be strongly predictive of expressive language abilities of autistic children at ages four (Stone & Yoder, 2001) and five (Thurm, Lord, Lee, & Newschaffer, 2007). Speech fluency at approximately eight years old was strongly related to parental reports and video evidence of motor abilities in the first two years of life (Gernsbacher et al., 2008); highly versus minimally verbal children were differentiated in early and later childhood by their ability to perform oral-motor tasks (e.g., sticking out the tongue, blowing raspberries and so forth), a deficit which appeared unrelated to problems comprehending instructions. Fine motor skills at 27 months predict expressive and receptive language at 45 months (Hellendoorn et al., 2015); furthermore, a large-scale study with over 1000 autistic individuals ranging from 2 to 15 found that this strong predictive relationship between fine motor skills and expressive and receptive language endures (Mody et al., 2017).[12] Another recent study corroborates the relationship between oromotor integrity and verbal development: Dalton, Crais, and Velleman (2017) reported a relationship, in autistic children, between their ability to sequence nonverbal mouth movements and their ability to sequence verbal mouth movements. Although the findings should be replicated in a larger sample, the authors also reported a relationship between joint attention and the ability to sequence nonverbal oromotor movements, which is pertinent to the current discussion given the noted relationship between joint attention and language development. Importantly, the relationship mentioned above between motor abnormalities and expressive and receptive language has also been demonstrated in HR infants (Bhat, Galloway, & Landa, 2012; Lebarton & Iverson, 2013; Leonard, Bedford, Pickles, & Hill, 2015). An atypical trajectory of vocal articulation and rhythmic arm movements in these infants has been suggested to reflect instability and atypical organisation within and between the motor and vocal systems (Iverson & Wozniak, 2007).

Our focus on motor deficits should not lead one to ignore the other non-motor deficits of ASC, most of which are well-known and intensely studied. These affect a broad range of skills ranging from social to mental-cognitive ones (Wing & Gould, 1979), and to perceptual and sensory abnormalities (Klintwall et al., 2011; Marco, Hinkley, Hill, & Nagarajan, 2011). That lack of motor movement and correlated motor-and-

sensory neural activity can entail deficits in integrating perceptions with actions is well known from experimental studies dating back to the famous work by Heid and Hein (1963), and some of the perceptual problems in ASC seem open to this explanation (e.g., inadequate response to social stimuli). We shall return to relationships between motor dysfunction and other autistic symptoms in greater depth below, but in so far as language is concerned, Wing (1981) commented on the constraint that motor dysfunction places on the developing autistic infant: "The limitation of his exploration and hence the poverty of concept formation would mean that his language would be repetitive rather than creative and that he would find abstractions hard to grasp" (p. 41).

This comment contains a central truth: that cognition shaped by environmental experience is person-centred and individualized (Casasanto, 2011; Hauk, 2011; Tschentscher et al., 2012; Willems et al., 2010). Commonalities in development lead to commonalities in conceptual organisation, but here, from very early life, the experiential field is vastly altered for individuals with ASC. In autism, the relationship between motor skills in toddlerhood and receptive and expressive language in childhood is mediated by reduced exploration of objects and environment and reduced social interest (Hellendoorn et al., 2015). It stands to reason that the emergent 'shape' of later cognition will diverge from the norm — and indeed, this is evinced by autistic abnormalities seen in semantic processing, organisation and categorisation (Dunn, Gomes, & Sebastian, 1996; Frith & Snowling, 1983; Gaffrey et al., 2007; Happé, 1997; Hermelin & O'Connor, 1970; Kamio & Toichi, 2000; Klinger & Dawson, 2001; Snowling & Frith, 1986; Toichi & Kamio, 2001, 2003; Wahlberg & Magliano, 2004). We aimed to probe the organization of conceptual knowledge with specific hypotheses based on the grounding of cognition in sensorimotor systems, and so expand, below, on the specific effect that motor impairment might place on action-semantic knowledge.

5. Motor systems and the mechanisms of action perception integration

"… if individuals move and respond in idiosyncratic ways from infancy, they will experience all interactions within a unique frame that most certainly differs from that which is called typical …" (Donnellan, Hill, & Leary, 2013, p. 3).

It now seems apt to discuss the role of motor systems in broader action cognition and action semantics, and to provide an explanatory neurobiological framework within which language and conceptual acquisition can be grounded in action and perception. To do so, we must consider the process by which, through associative learning and linkage with other neural populations, cells within action perception circuits become infused with multimodal sensorimotor properties. These multimodal cells consequently become involved in new cognitive processes, such as conceptual understanding, whilst retaining their original functional roles. This process, called 'information mixing' (Braitenberg & Schüz, 1998), 'neural

---

[12] This study differentiates between gross and fine motor skills and also finds predictive relationships between gross motor skills and expressive language, and between gross motor skills and receptive language in a subset of children with particular impairments in gross motor skills. The authors suggest that the relationship between language abilities and fine motor skills, as are indicated in the studies here, are more robust than relationships with gross motor ability; however, the study does illustrate the importance of the measures used, as they include a performance-based measure of fine movement skills and a parent report of gross movement skills.

exploitation' (Vittorio Gallese & Lakoff, 2005) or 'neural reuse' (Anderson, 2010), characterizes the well-established finding of multimodal neurons which carry information across different modalities, including motor, visual and auditory feature processing. Action perception integration is simply illustrated in the following example, where sensory and motor populations of neurons increase the efficacy of their mutual connections due to correlated activity (Hebb, 1949). In addition, the stronger links will provide additional recurrent activation in action production (because sensory neurons now receive activity from the motor side and channel it back to motor neurons) and in the perception process (because the once-sensory-only neurons are now infused with recurrent motor activation). Thus, the neurons on the motor (/sensory) side of the network also take a role, and have a functional influence, in the respective other process (sensory neuron in production and motor neuron in perception). Ultimately, the stronger connections in the entire population (which are likely to include neurons in other areas, too) yields activity maintenance after stimulation, due to reverberant activation supported by the strong population-internal links. This explains the "emergence" of higher cognitive processes, such as working memory (Shebani & Pulvermüller, 2013), from sensory and motor mechanisms. Simulation studies bolster this kind of information mixing, leading to integration of specific information about actions and perceptions and, ultimately, "neural reuse" of the same neurons for cognition.

From this perspective, the great significance of mirror neurons comes from the fact that they demonstrate information mixing in action processing. These neurons within motor systems (motor and premotor cortex) are bound into distributed circuits that also include sensory neurons and thus can be activated through sensory stimulation (for example, observing or hearing an action). Multimodal cells are however also extant outside of the cortical motor system, in particular in prefrontal and a range of parietal and temporal areas (Fuster, 2003; Molenberghs, Cunnington, & Mattingley, 2012; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). These findings situate action perception integration across the majority, if not all, cortical regions.

Whether some such information-mixing neurons are innately specialised and present from birth is still a matter of debate (Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011). However, it seems uncontroversial that, in early life, an infant's repetitive body movements, and the concurrent activation of both motor neurons controlling the action along with somatosensory and visual neurons processing its sensory consequences, evoke correlated activity across sensory and motor areas of cortex; and furthermore that, following Hebbian mapping of correlated neuronal activity (Palm, Knoblauch, Hauser, & Schüz, 2014), this will lead to strong links between neurons distributed across sensory, motor and multimodal areas, which sit adjacent to primary motor and sensory regions. In Section 4 above, we have already summarized the implications of early babbling for the initial creation of action perception circuits linking the articulatory programmes for producing syllables and words with their corresponding tactile and acoustic-phonological features. These may be made possible via the neuroanatomical long-distance connections between motor (frontal) and sensory

(temporoparietal) regions, which are particularly richly developed in humans (Pulvermüller & Fadiga, 2010). These may indeed contribute to an explanation why human language and sociocommunicative interaction is much more complex than that seen in primates (Schomers et al., 2017).

Beyond the action perception circuits formed through early babbling, how might words be mapped to meaning? Pulvermüller (1999, 2012) describes semantic learning in the context of social interaction in the presence of relevant objects and conceptually related information in the environment, for example when an object is named by an adult whilst the child explores its sensory features (for details about this form of learning, see Smith, Suanda, & Yu, 2014). Similarly, words for actions are frequently learnt in the 'grounding' context of performing these actions (Tomasello & Kruger, 1992). This correlated neural activity means that the perisylvian cell assemblies storing a word's articulatory and phonological properties are extended to incorporate extrasylvian perceptual and action systems (Pulvermüller & Fadiga, 2010). As these 'semantic circuits' carry conceptual information related to a word's referents, they may differ topographically depending on the semantic meaning of the word. Words with action-related meaning incorporate neurons representing motor programs in frontal and motor areas, thus resulting in the somatotopic effector-specific activation discussed in Section 1. In contrast, occipitotemporal cortex is activated by visually-related object words (Martin, 2007), and auditory, olfactory and gustatory regions by sound-, smell- and taste-related words (see, for example, Barrós-Loscertales et al., 2012; Chao & Martin, 1999; Goldberg, Perfetti, & Schneider, 2006; González et al., 2006; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Kiefer et al., 2012; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Moscoso Del Prado Martín, Hauk, & Pulvermüller, 2006; Simmons et al., 2007).

Typical and *optimal* semantic processing may require the collaboration of modal systems with cross-modal 'hubs' or 'convergence zones', a putative substrate of which may exist in anterior temporal lobe (Garagnani & Pulvermüller, 2016; Humphreys, Hoffman, Visser, Binney, & Lambon Ralph, 2015; Kemmerer, 2015; Lambon Ralph, Ehsan, Baker, & Rogers, 2012; Pobric, Jefferies, & Lambon Ralph, 2010; Pulvermüller et al., 2010; Rice, Ralph, & Hoffman, 2015; Tomasello, Garagnani, Wennekers, & Pulvermüller, 2016; Simmons & Barsalou, 2003; Tomasello, Garagnani, Wennekers, & Pulvermüller, 2017; Visser, Jefferies, & Lambon Ralph, 2010; Visser, Jeffries, Embleton, & Lambon Ralph, 2012). Within this 'spoke and hub' approach, a body of neuroscientific evidence strongly supports the functional importance of sensorimotor activation itself for understanding the meaning of words (see literature cited in first section and Schomers & Pulvermüller, 2016, for review). It is these investigations of the *necessity* of such activation for conceptual processing that highlight where ASC may demonstrate the dependence of higher cognitive functions on frontotemporal and sensorimotor links. The striking impairments of autistic individuals in movement and action cognition, along with their brain abnormalities in the motor systems and their differential relationship with the environment during development (Hellendoorn et al., 2015), motivated investigations of language processing in this population. If motor systems and

their connections to other brain regions are abnormal in ASC (see Section 2 and 3), this would affect the coupling between action and perception systems (demonstrated in Sections 2 and 3) and the neural reuse of this coupling for language and cognition. It should become difficult to build action perception circuits for spoken and written word forms, thus predicting a general linguistic processing deficit. Although all words possess articulatory and phonological sensorimotor properties (i.e., they can be spoken and heard), some words possess additional links to motor systems according to their semantic association with actions. As such, individuals with ASC may exhibit a particularly pronounced processing problem with these items which especially draw on motor regions for retrieval of meaning.

As mentioned, mirror neurons are suggested by some to play a critical role in the representation of action goals and thus action and intention understanding (Di Cesare et al., 2015; Rizzolatti & Sinigaglia, 2010) and in accordance with this view may, we suggest, receive their multimodal character through information mixing consequent to being part of action perception circuits. Incorporated into cell assemblies for language, we suggest these cells contribute specific articulatory motor and/or action-related semantic information about meaningful words (and also action sounds). We must return briefly, here, to some of the controversies surrounding the function of these cells: specifically relating to the claim (originally by Mahon and Caramazza (2008) and later by Hickok (2014, 2010) and Mahon and Hickok (2016)) that motor (mirror) areas are activated by action words not because of their role in representing and processing action meaning, but instead because neural activation spreads there from some other regions where meaning is actually being processed. Although this represents a theoretical possibility that the low temporal resolution of functional magnetic resonance imaging (fMRI) cannot refute, much of the available evidence presented in Section 1 strongly refutes this suggestion. However, another argument against motor system involvement in action semantics is predicated by cases in neuropsychology where action word processing is not completely disrupted by disease or lesion to the motor systems (Hickok, 2010, 2014). We cite evidence of action word processing abnormalities in patients with motor damage in Section 1, but this is an important point which we explore in full below, where we link action word deficits to motor system dysfunction in ASC.

6. Autistic 'disembodiment' of action semantics; a test of motor involvement in action word processing

Given their abnormalities of motor function and motor systems, the abnormalities of mirror neurons during action perception, and abnormalities of cortical communication, individuals with autism were considered a strong test case to examine the functional importance of motor systems in action semantics, specifically the processing of words with action meaning (e.g., 'jump'). We proposed that the aforementioned dysconnectivity within and between motor systems and other cortical regions, which is linked to impaired visuomotor or action perception integration in

motor tasks (see Sections 2 and 3), would give rise to a similar lack of action perception integration in the language domain. The model of action perception integration during language learning, set out above, generated clearly testable hypotheses:

1. That compared with TD individuals, people with ASC would show reduced activity in motor systems when processing words with action meanings;
2. That at the behavioural level, compared with TD individuals, people with ASC would show a specific deficit or less efficient processing of words with action meanings;
3. That if activity in motor areas is functionally relevant for semantic processing of action words, there should be a relationship between brain and behavior.

To test these predictions, Moseley, Mohr, et al. (2013) compared brain activity to action and object words in eighteen adults with ASC (mean age: 30) and eighteen age- and IQ-matched controls using fMRI. Participants engaged in a passive reading task where they were asked to read words as they flashed up on the screen; no behavioural responses were required and any movements were discouraged. Whole brain and regions of interest analyses revealed strong frontocentral activation to words in TD individuals, but general frontocentral hypoactivity in ASC (see Fig. 1 Part A). These findings are consistent with full ignition of frontotemporal circuits for words in control participants, but partial failure of ignition in ASC, specifically in the frontal and motor components of these circuits. Note again that much neuroimaging and neuropsychological work suggests that in TD participants, the frontotemporal (including motor) areas activate even if participants perceive meaningful language passively (e.g., D'Ausilio et al., 2009; Shtyrov et al., 2004, 2014; Wilson, Saygin, Sereno, & Iacoboni, 2004).

As noted in the neurobiological model of word processing outlined above, words with action-related meaning (e.g. 'jump') are expected to involve motor systems much more than words typically used to speak about objects, as in addition to articulatory phonological knowledge, they ignite action-related semantic knowledge that is bound to the word form. Subsequently, in addition to generally reduced motor system activity during word processing, we observed a specifically strong hypoactivity for words semantically related to action (Fig. 1 Part B) — as predicted in hypothesis 1, above. A region-of-interest analysis (ROI) comparing autistic and non-autistic participants found no difference in activity evoked by object words in precentral gyrus, but a significant difference in the activity evoked by action words in precentral gyrus, which was lower in ASC.

To examine the functional role of this motor activity in action word processing, we invited the same autistic participants who had taken part in the neuroimaging experiment to come back to the lab a few weeks later. Here, they completed a semantic decision task where they made speeded semantic decisions about the meaning of the words previously presented in the fMRI experiment. When comparing semantic decision performance for action and object words (which were matched for a range of psycholinguistic features), we found that individuals with ASC processed action-related words significantly more slowly than object words. TD individuals
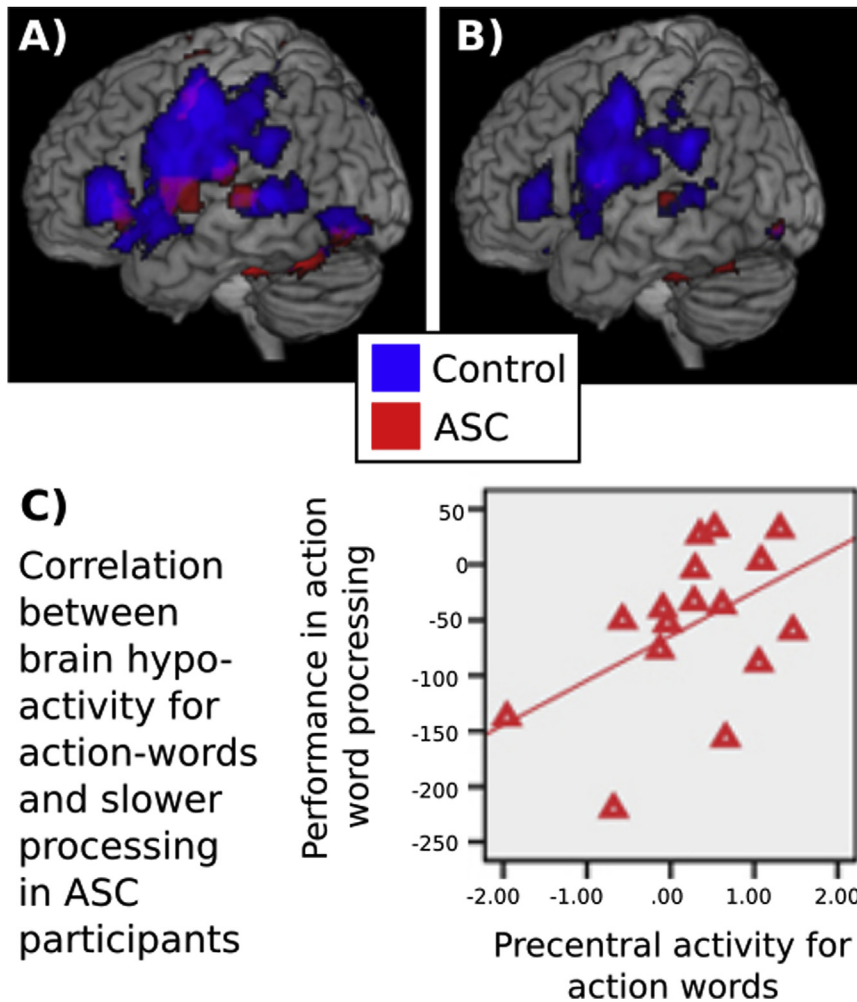
Fig. 1 – Data from **Moseley, Mohr et al. (2013), Moseley, Pulvermüller, et al. (2013)**. **Participants engaged in a silent reading task where they passively read a large corpus of words including abstract words (such as 'peace'), object words ('cheese') and action words ('kick'). In Panel A, overlays of brain activation for the contrast of all words versus a low-level visual baseline (hash-marks) are depicted for the control (blue) and ASC participants (red), at an uncorrected threshold of p < .005. In Panel B, overlays of brain activity for action words versus a low-level visual baseline (hash-marks) for controls (blue) and ASC participants (red), p < .005 uncorrected. Panel C depicts the correlation in ASC participants between hypoactivity in a precentral region-of-interest and poorer processing of action words (quantified by subtracting response times for matched object words, which autistic participants were quicker to process, from reaction times to action words). Lower scores in this axis therefore depict a greater deficit in action word processing as compared to object words.**

were equally efficient in processing both types of words. Consequently, hypothesis 2, above, was supported.

From a theoretical perspective, hypothesis 3 is perhaps the most important for evaluating a functional role for motor systems in action word processing: if hypoactivity in this region is related to problems in understanding, this would be strong evidence for a semantic function of this region. In autistic participants, the level of activity elicited in frontal motor systems by action words indeed correlated significantly with the specific processing deficit for these words (Fig. 1 Part C), which provides strong evidence for hypothesis 3.

On reporting a behavioural deficit in action word processing in autism, it is important at this point to revisit the neural architecture facilitating this kind of action perception integration in humans. The failure of perceived words to ignite

activation in frontal and motor systems, in autism, is consistent with the general disruption of long-distance cortico-cortical communication in ASC and furthermore with the dysconnectivity within and between motor systems and other brain regions. The impaired integration of motor and perceptual information shown here in the language domain most particularly implies deficits in the long-distance fibre bundles that are especially important in the sensorimotor 'information mixing' process for language. The arcuate fasciculus (AF) has been purported to play a particular role in channelling sensory activity in temporal and parietal regions to the frontal lobe and motor cortex (Pulvermüller & Fadiga, 2010; Schomers et al., 2017). We thus conducted probabilistic tractography (diffusion-weighted imaging) of the long frontotemporal segment of the arcuate in 18 adults with AS and 14

age- and IQ-matched TD controls. This analysis revealed a substantial bilateral reduction in the volume of this neuro-anatomical connection bundle (Moseley et al., 2016: see Fig. 2). Abnormalities in the arcuate were also found in two other studies, one with a larger population of autistic adults (Catani et al., 2016), another in a population of autistic children (Roberts et al., 2014), though in both studies abnormalities were left-lateralised.

That a relationship exists between behavioural processing deficits and hypoactivity in brain regions argued to support action semantic meaning is strong evidence for a functional role of motor systems activity in action word processing. Another argument against an epiphenomenal interpretation of Moseley, Mohr et al.'s (2013) findings comes from a follow-up study where participants completed the same silent reading task during combined EEG-MEG recording. In typically-developed individuals neurophysiological distinctions between action and object words are evident within 150 msec of word presentation (Moseley, Pulvermüller, et al., 2013). Distinctions between different types of action words are likewise evident between 150 and 200 msec (Pulvermüller, Shtyrov, et al., 2005), sometimes even earlier (Shtyrov, Butorina, Nikolaeya, & Stroganova, 2014). These studies, along with many others, refute the possibility that sensori-motor semantic activity reflects a process secondary to language understanding, because other work has shown that the earliest semantic activations in well-established, multimodal semantic areas appear at the same time, at around 100–200 msec (e.g., Boulenger, Shtyrov, & Pulvermüller, 2012). The same paradigm in autistic participants showed a marked lack of sensorimotor activity for action words in frontal cortices (in fact, greater activity for object words here), and indeed a general lack of distinction between action *and* object words at this early stage of processing (Moseley et al., 2014).

This behavioural and neuroscientific evidence, along with previous studies of patient groups (see Section 1), strongly suggest a functional role for motor systems in action semantic processing. It is however notable that our highly capable autistic adults were slower but *not less accurate* than control participants in the processing of action words. That they were correct in their semantic decisions on action-related words suggests a deficit in efficient access to action-semantic information. Indeed, we return here to the argument offered by Hickok (2014) above, and would suggest that the evidence supports the necessity for motor system involvement in optimal action word processing, but does not deny the possibility of other means of retrieving semantic information (see Pulvermüller, 2013). We would suggest that the linkage between motor and perceptual regions in ASC is certainly not entirely 'broken' (as has been well argued by others as far as mirror neurons are concerned [Hamilton, 2013]), but it rather appears that the integrity of action perception circuits is reduced, as would certainly be suggested by reduced integrity of corticocortical connectivity. A reliance on more perceptual or combinatorial modes of semantic processing could be supported by temporal or parietal areas such as, for example, the anterior temporal lobe's so called semantic 'hub'; this might allow retrieval of meaning but not with the same speed and proficiency. Alternate routes of processing, in ASC, are

consistent with less automatic semantic processing compared with TD individuals (Frith & Snowling, 1983; Happé, 1997; Jolliffe & Baron-Cohen, 1999; López & Leekam, 2003; Wahlberg & Magliano, 2004; Jarvinen-Pasley et al., 2008). This may explain why a silent reading task might not elicit efficient access to action semantic information in people with ASC whilst they prove capable of processing these words by alternative means – such as reliance on additionally recruited visual cortices (Gaffrey et al., 2007). Alternative routes by which people with ASC might retrieve action meaning *in vivo* are yet to be identified: an important goal for research clarifying the retrieval of conceptual meaning.

In concluding this section, we refer to the causal interpretation paradigm normally applied in neuropsychology, where neuronal abnormality is presumed to be the cause of behavioural deficits or deviance from the norm. An important result of the research above (Moseley, Mohr et al., 2013) was that access to action semantic knowledge was gradually related to the degree of precentral activation of the motor system, reflecting a correlational relationship between motor activity and comprehension performance. Although correlations in themselves prohibit conclusions on causality, we posit that the specific neurobiological features of ASC, manifest in hypoactivation of the motor system during action word comprehension, are a plausible cause of the correlated efficiency reduction in action semantic processing. This position is grounded in the previous literature suggesting a) functional importance of this area for action semantic processing (see Section 1) and b) structural abnormalities, in ASC, in frontal motor systems, their internal connections and those connecting them to other brain regions, particularly the long-distance pathways between temporal and parietal circuits involved in perception and frontal and motor circuits important for action processing (Catani et al., 2016; Moseley et al., 2016; Roberts et al., 2014). We suggest that consequently, the developing circuits binding action- with perception-related information are fragile in ASC and do not efficiently channel perceptual information to motor circuits. At the behavioural-cognitive level, this lack of frontotemporal action perception binding and reduced comprehension-related motor activation was here manifest in a specific sluggishness during action semantic processing. As relates to the cognitive neuroscience of semantic processing, we finally postulate that these correlation results from ASC are strong evidence for the functional relevance of motor systems for processing words with action-related meaning. This conclusion does, however, lead to further testable hypotheses which were examined in the study discussed in the next section: how would individuals with ASC perform with other words which draw on motor systems for meaning?

7. Abstract emotional meaning and autism; the case of emotion words

"Ein innerer Zustand bedarf äußerer Kriterien" [An inner state requires external criteria] (Wittgenstein, 1953, *Philosophical Investigations*, 580)
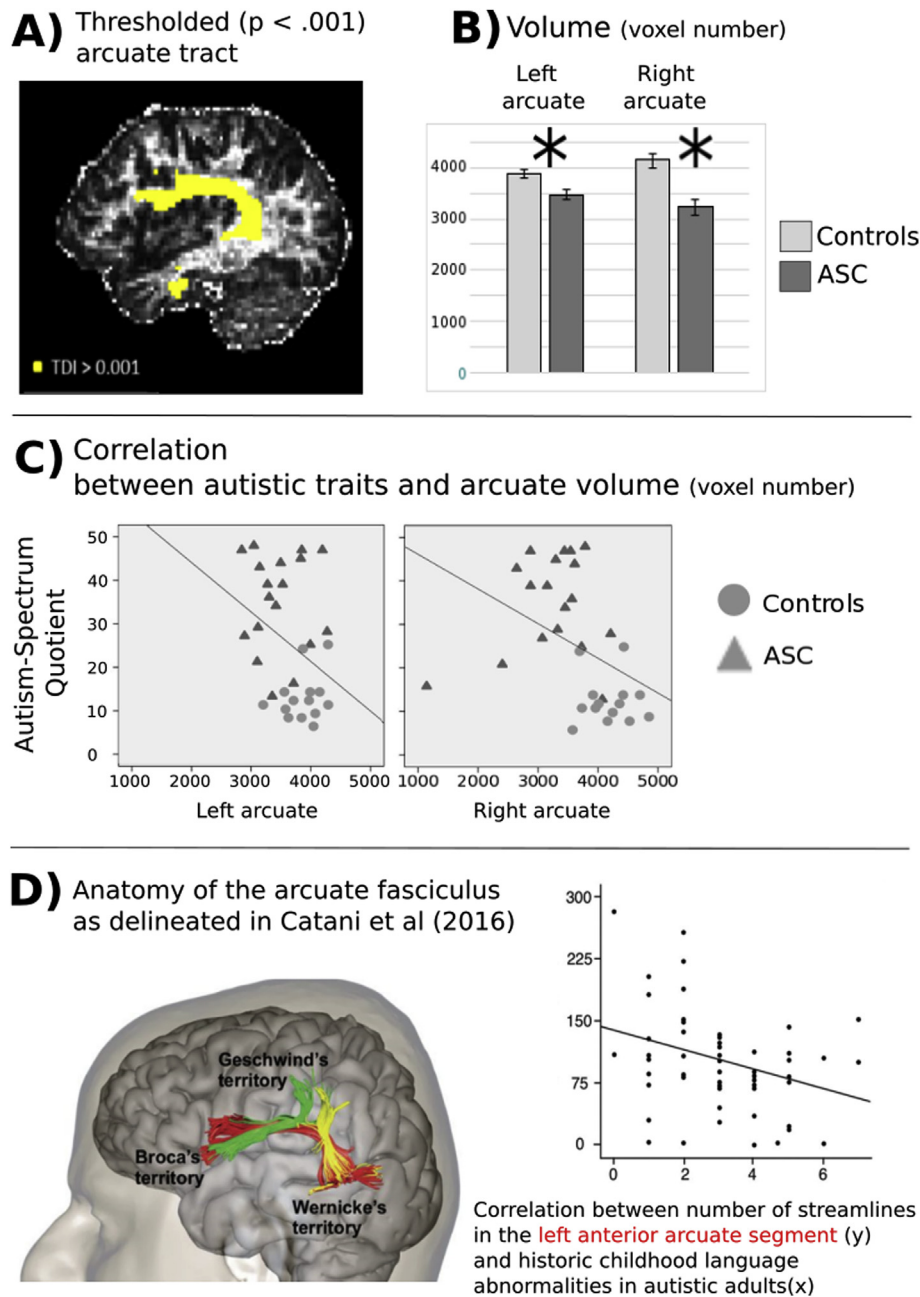
A) Thresholded (p < .001) arcuate tract

B) Volume (voxel number)

C) Correlation between autistic traits and arcuate volume (voxel number)

D) Anatomy of the arcuate fasciculus as delineated in Catani et al (2016)

Correlation between number of streamlines in the left anterior arcuate segment (y) and historic childhood language abnormalities in autistic adults(x)

Fig. 2 – Panels A to C show selected findings of volumetric reduction in the arcuate fasciculus in people with ASC (Moseley et al., 2016); Panel D shows figures reproduced with permission of Catani et al. (2016). Part A shows a thresholded (p < .001) mask of the arcuate fasciculus in a single participant. Part B reflects average volume (voxel number) of the arcuate fasciculus for autistic and control participants in the left and the right hemisphere, with asterisks reflecting significant group differences. Part C reflects correlations between autistic traits, as measured by the AQ: Baron-Cohen et al., 2001, and volume of the arcuate fasciculus in the left and right hemispheres. A significant correlation between autistic traits and right arcuate volume (r = −.413, p = .019) reflected that reduced arcuate volume was associated with a higher number of autistic traits. The same pattern was marginal in the left hemisphere (p = .056). Interestingly, we note that whereas our results showed bilateral reduction in the arcuate which was most apparent in the right hemisphere, other analyses found abnormalities in the left hemisphere only (Catani et al., 2016; Roberts et al., 2014). Catani et al., who studied a large adult sample, found reduced fractional anisotropy in the arcuate fasciculus (and some other frontal tracts): this measure reflects reduced microstructural integrity (via less restricted diffusion along the tract), and is thought to reflect differences in fibre density, axonal diameter and myelination of white matter. Panel D shows figures reproduced from Catani et al. As well as finding abnormalities in the long segment of the arcuate, which is here shown in red and appears approximate to our delineation of the whole arcuate tract, these authors found a relationship between the frontoparietal "anterior" segment of the left arcuate (shown in green, which we suggest may be equivalent to what others have described as the third branch of the superior longitudinal fasciculus [see Moseley et al., 2016, for discussion]) and stereotyped, repetitive and idiosyncratic speech in childhood as measured by item B3 of the Autism Diagnostic Interview-Revised (Le Couteur et al., 2003).

The disruption of action perception circuits supporting word meaning predicts particular impairment, in autism, for language and especially for any words whose meaning draws on motor systems. The most typical case of action words, in this sense, are signs used to speak about actions that language-using humans normally perform by themselves (e.g., 'write', 'lick'). The learning of these words is possible in the context of performing the action overtly, watching others do so, or when the context leads to a 'simulation' of the actions in the mind and brain. The situation is much more complicated in the case of abstract emotion words, and possibly in the case of all abstract words, which, according to Vigliocco et al. (2014), are often emotion-related. Abstract emotion words need to be related to an 'inner state', but problematically such an inner state would not be directly accessible to the teacher who could teach the language-learner the correct use of emotion words. This issue is a crucial one in the philosophy of language and mind, where one simple solution has been offered: that the language-learning child normally expresses its 'inner' emotional states (e.g., joy, fear) in its actions, which provide the key for the language-teacher to link the word to its correct meaning (Wittgenstein, 1953). Abstract emotion words would thus behave like 'hidden' action words, and would be linked with meaning through embedding (expression) in action.

Indeed, an fMRI study investigating the processing of emotion words (such as 'joy' and 'fear') showed activity not only in limbic emotion-processing areas (such as anterior cingulate and anterior insula), reflecting the affective meaning of these terms, but in motor areas overlapping with regions activated by overt action-related words (such as "write" and "lick"; Moseley, Carota, Hauk, Mohr, & Pulvermüller, 2012).

Throughout life, individuals with ASC show fundamental differences in their expressions of emotion. Emotional expression in the face and voice is typically described as reduced or absent (Kanner, 1943; Moody, McIntosh, Mann, & Weisser, 2007; Scambler, Hepburn, Rutherford, Wehner, & Rogers, 2007; Yirmiya, Kasari, Sigman, & Mundy, 1989) or as markedly atypical and less recognisable (Asperger, 1944; Kanner, 1943; Langdell, 1981; Loveland, Tunali-Kotoski, Pearson, Brelsford, & et al., 1994; Mcdonald et al., 1989; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Moody et al., 2007). This would make it particularly difficult for language-teachers to teach autistic children abstract emotional meaning in the means described above, and predicts a specific deficit in the processing of abstract emotion words comparable to that documented for (other) action words above.

It was on this basis that we examined emotion word processing in autistic participants (Moseley, Shtyrov et al., 2015; Moseley, Ypma et al., 2015). We observed a similar 'disembodiment' of emotion concepts, which failed to activate either motor systems or limbic systems as they did in controls (see Fig. 3). Importantly, hypoactivity was specific *in these regions* and specific to *abstract emotion verbs* such as 'fear'; no group differences were seen in analysed regions for abstract verbs such as 'dwell' or 'waive'. As these words were matched in concreteness, imageability, frequency and familiarity, this category-specific brain difference could not be associated with
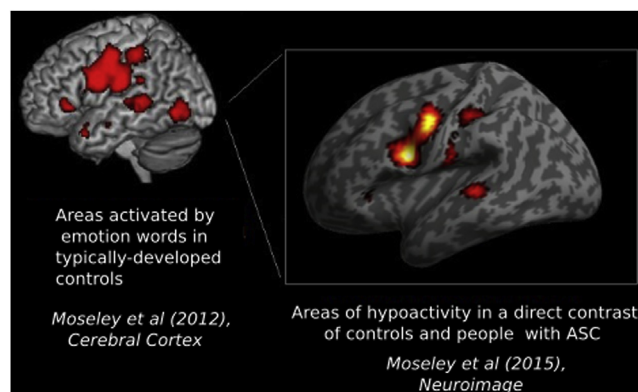

Fig. 3 − **Activity evoked by emotion words in typically-developing individuals, and areas of autistic hypoactivity in a direct contrast of emotion-word activation in controls and individuals with ASC. The uncorrected (p < .005) image on the left depicts brain areas activated in a comparison of abstract emotion words (such as 'fear') versus a low-level visual baseline (hashmarks) in typically-developing controls. The image on the right, which is corrected at the FWE rate (p < .05), depicts areas significantly more active in controls than people with ASC when viewing the same emotion words.**

the highly abstract nature of emotion words. Nor could it be said that people with ASC showed a general deficit for all *verbs*, since a dissociation appeared within the grammatical category, specifically for words with mental-state content.

Interestingly, the degree of motor hypoactivation for emotion words seen in individual autistic participants predicted their degree of autistic traits as assessed by the Autism-Spectrum Quotient (AQ) (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). This is in fact consistent with the idea that abstract emotion words can be seen as semantically similar to action words insofar as being learnt via similar mechanism − because for overtly action related verbs like 'lick' and 'write', an association was found where hypoactivity in motor systems correlated with higher numbers of autistic traits (Moseley, Mohr et al., 2013). This is an important finding which we return to below.

The neurobiological indication for reduced semantic-related motor activation for emotional language in ASC ties in nicely with behavioural work on language understanding. Difficulties in understanding and using words denoting internal states have been well documented in autism (Baron-Cohen et al., 1994; Happé, 1994; Jolliffe & Baron-Cohen, 1999; Tager-Flusberg & Sullivan, 1994; Tager-Flusberg & Sullivan, 1995; Tager-Flusberg, 1992). Such indication that emotional language processing is reduced also sits nicely with evidence for more general autistic difficulties in emotion recognition in both verbal and nonverbal stimuli (Harms, Martin, & Wallace, 2010; see Uljarevic & Hamilton, 2013, for a more nuanced view). To what degree motor and limbic cortices are causally involved in emotion and emotion word processing is an exciting focus of current investigation. Several studies indicate a causal link between implicit simulation of emotions in the individual and recognition of those same emotions in

others (Bastiaansen, Thioux, & Keysers, 2009; Baumeister, Papa, & Foroni, 2016; Goldman & Sripada, 2005; Neal & Chartrand, 2011; Oberman, Winkielman, & Ramachandran, 2007; Stel & van Knippenberg, 2008; Wood, Rychlowska, Korb, & Niedenthal, 2016). Studies have also shown that basic movement kinetics, processed atypically in ASC, offer clues to the emotional and mental states of others (Hubert et al., 2007; Patel, Fleming, & Kilner, 2012). In the language domain, processing of emotion-related language is affected by manipulation of facial musculators (Glenberg, Havas, Becker, & Rinck, 2005; Havas, Glenberg, Gutowski, Lucarelli, & Davidson, 2010) or damage to white matter just adjacent to motor cortex (Dreyer et al., 2015). This evidence implies a potentially causal link between the motor hypoactivity we observed in ASC during processing of emotion words, and the emotion word processing deficits noted above in behavioural studies. This requires further investigation, though we return, below, to a wider role for motor systems in emotion understanding and recognition generally.

8.   Widening the lens: autism as a disorder of movement and action perception integration

"In an infant or a toddler, the possible effects of slow responding or delayed initiating would surely have an effect on the entire trajectory of development … [and on] the 'dance of relationships' (Stern, 2000)" (Donnellan et al., 2013, p. 6).

The recent research summarized in the previous sections has focused on the role of sensorimotor systems and action perception integration in language and semantics and the differences observed between autistic and TD participants. We would however like to return here to a finding which may initially appear as an accidental observation but which may reflect core aspects of ASC with great theoretical significance: the observed hypoactivity of motor cortex during language understanding generally, and particularly in action and emotion word processing, and the significant correlation between this hypoactivity and the number of autistic traits an autistic person exhibits. Autistic individuals with greater impairment in social interaction, more repetitive and restricted interests and lack of imagination (as measured by the AQ: Baron-Cohen et al., 2001) showed the greatest degree of hypoactivity, ergo, abnormality in motor systems and action perception integration (Moseley, Mohr et al., 2013; Moseley, Shtyrov et al., 2015; Moseley, Ypma et al., 2015). This is a finding which resonates with those of other research groups: Nebel, Eloyan et al., 2014 found the extent of atypical functional connectivity in precentral gyrus to predict diagnostic status, ASC severity (as measured by the Autism Diagnostic Observation Schedule [Lord et al., 2000]) and sociocommunicative skills (measured by the Social Responsiveness Scale [Constantino et al., 2003]). Catani et al. (2016) reported a relationship (see Fig. 2, Part D), in their autistic participants, between the degree of abnormality in the arcuate and uncinate fasciculi and childhood language symptoms as measured by the Autism Diagnostic Interview-Revised (Le Couteur et al., 2003). At the behavioural level, relationships

between movement deficits and autistic symptom severity are well documented in our review (MacDonald, Lord, & Ulrich, 2014; MacDonald, Lord, & Ulrich, 2013; Papadopoulos et al., 2012; Stevenson, Lindley, & Murlo, 2017; Travers et al., 2015, 2013; Uljarevic, Hedley, Alvares, Varcin, & Whitehouse, 2017; Colombo-Dougovito & Reeve, 2017 are an exception, but a questionable one due to their methods).

A link between motor disorder and the broader symptoms of autism was to our knowledge first proposed by Leary and Hill (1996), who pointed out the seemingly obvious detrimental effects of movement abnormalities on speech, emotional expression, social interaction and communication with others. These authors produced a radical but little noticed reimaging of the 'autistic triad'. Their thesis received little support in the 1990s but was followed by consideration of an 'enactive mind' approach by Klin, Jones, Schultz, and Volkmar (2003), according to which "… social cognitive processes emerge only from recurrent sensorimotor patterns that allow action to be perceptually guided" (p. 350). With reference to a vast array of eye-tracking data, these authors suggested that, in ASC, 'disembodied' routes are taken for generating social responses instead of the normal 'embodied' pathways, hence their unnatural and often inappropriate quality, and that this might result from a lack of salience to social stimuli from very early life. "The tools of thought are acquired outside the realm of active social engagement and the embodied experiences predicated by them" (p. 357). Klin et al.'s account spoke of the grounding of social processes in experience, but did not strongly highlight the necessary integrity of motor and sensory systems along with their structural connection for the typical development of thought and social behaviour. At the time, much less was known about fundamental dysfunction in sensorimotor and neuronal systems in ASC, such as the motor abnormalities that have been outlined in Sections 2 and 3 above or the sensory abnormalities that are the focus of other papers (Klintwall et al., 2011; Marco et al., 2011).

The connection between fundamental sensorimotor disruption and higher cognitive and social impairments has since been made more explicit by other theorists such as Eigsti (2013), who drew a putative link between movement deficits in ASC and impairments in motion perception, mimicry (including the very automatic, implicit form that is contagious yawning) and gesture. Mostofsky and Ewen (2011) extend this link to imitation, praxis and ToM (see further discussion below). In addition to the empirical evidence presented in these accounts, a number of studies have demonstrated that movement disorder may indeed have predictive value for autistic symptoms more broadly than the aforementioned prediction of language development (Bhat et al., 2012; Donnellan et al., 2013; Gernsbacher et al., 2008; Hellendoorn et al., 2015; Lebarton & Iverson, 2013; Stone & Yoder, 2001; Thurm et al., 2007). At a broader level, motor skills at age two are the strongest predictor as to whether these children would still meet diagnostic criteria for ASC at age four, where language, communication, socialisation skills and symptom severity were still non-significant (Sutera et al., 2007). Another study found that at six months of age, head-lag (inability to keep the head in line with the spine when infants are pulled upright from a supine position, indicating weak head and neck control) is predictive of an ASC diagnosis and of delays in

social development and communication at 30 or 36 months (Flanagan et al., 2012). Similarly, MacDonald, Lord, and Ulrich (2014) found both fine and gross movement impairments between the ages of 14—33 months to predict the severity of autistic symptoms (in the sociocommunicative domain). These results all strongly suggest that motor impairments are one of the earliest predictors of autism and thus may be a crucial (though not necessarily syndrome-specific, given their appearance in other developmental conditions [Gillberg, 2010; Levit-Binnun, Davidovitch, & Golland, 2013]) early signifier of aberrant brain development.

Furthermore, Leonard et al. (2014) found movement delay or impairment at nine months predictive not only of movement disorder at 5—7 years old but also predictive of difficulties interpreting facial expression and gaze direction at the same age. Interestingly, movement impairment was no longer predictive of these social-cognitive skills at forty months, with the authors hypothesising a potential 'critical period' in which development of face processing ability is most strongly influenced by lagging or intact motor development. Several studies in older autistic children (Dyck, Piek, Hay, & Hallmayer, 2007; Hilton et al., 2012; Hilton et al., 2007; Sipes, Matson, & Horovitz, 2011), and indeed non-autistic children (Bar-Haim & Bart, 2006; Cummins, Piek, & Dyck, 2005; Piek, Bradbury, Elsley, & Tate, 2008; Whittingham, Fahey, Rawicki, & Boyd, 2010), also report correlations between motor dysfunction, social impairments and even emotion recognition.

In a broader perspective, such evidence is indicative of a crucial role for motor systems and action perception integration in typical cognitive and social development. A child with motor impairments cannot effectively link perceptual precedents and consequences to its own motor activities, and therefore will have difficulty interacting with the external world and other agents with the same ease and flexibility. Among other problems, motor impairments would cause difficulties exploring the environment, manipulating objects, looking at others, and producing communicative attempts. With limited motor ability, it already becomes more difficult to perform the aforementioned elementary rhythmic extremity movements and babbling articulations, in the second half year of life, which may be so crucial for setting up connections between action and perceptual brain circuits and serve later as a vehicle for repetitions. Incidentally, as we have seen in Sections 2 and 4, the ability to repeatedly articulate verbally (in babbling) and to move are amongst those early deficits present in autistic infants, and the resultant reduced production of vocal and motor acts has implications for the development of further social and cognitive domains, including empathy (Braadbaart, de Grauw, Perrett, Waiter, & Williams, 2014; Decety & Meltzoff, 2011; Meltzoff & Decety, 2003). Needham and Libertus (2011) link the development of reaching behaviours to the ability to interpret others' reaches as goal directed; the ability to crawl to that of representing space in a non-egocentric or allocentric manner; the ability to sit and reach and thus take part in hiding games to object permanence. Crawling and standing opens up many new possibilities for social interaction (Campos et al., 2000; Clearfield, 2011; Karasik et al., 2014). If reconceptualising the symptoms of ASC in light of the relationship between motor dysfunction and autistic

symptomatology, a startling and unexpected finding is that ability to reach for objects or faces, at three months old, actually itself increases spontaneous interest and orientation towards faces (Libertus & Needham, 2011). This finding is particularly notable in light of a popular model of autism which attributes causal primary of symptomatology to abnormalities in social motivation (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012). Differences in social orienting and attention have been reported along with motor abnormalities within the first year of life (Clifford, Hudry, Elsabbagh, Charman, & Johnson, 2013; Maestro et al., 2002; Ozonoff et al., 2010; Saint-Georges et al., 2010; Zwaigenbaum et al., 2005). A putative connection between motor dysfunction and decreased social inclination is self-evident to a degree but it remains to be shown whether key social deficits can be explained in terms of action perception integration.

Eigsti (2013), in a thorough review of a potential role for 'disembodiment' in autistic symptomatology, called for "direct tests of embodied processes" (p. 7); she subsequently provided one, demonstrating that encoding Japanese characters in an avoidance or approach position affected how positively TD individuals rated that same stimulus later, but did not affect individuals with ASC (Eigsti, Rosset, Col Cozzari, da Fonseca, & Deruelle, 2015). Likewise, the experimental series on semantic understanding summarized in Sections 6 and 7 above are consistent with the view that, to use Eigsti's words, "the stimuli that an individual with [ASC] encounters may be less bound to the sensory and motor conditions that held when that stimulus was first encountered" (p. 7). The role of sensorimotor systems in linguistic and socio-communicative processing, and indeed this reframing of autistic symptomatology, encourages scientists to search for further roles for sensorimotor cortical systems in other kinds of cognitive processes. We consider briefly, here, some avenues worthy of research attention.

One sociocognitive process with particular resonance for ASC is theory of mind, or ToM (Baron-Cohen, 2009; Senju, 2013): an impairment in the process by which we think about (predict, estimate and infer) the mental and emotional states of others appears to set people with ASC apart from individuals with developmental conditions such as ADHD (Gonzalez-Gadea et al., 2013). Typical tests of ToM emphasise the understanding of action in social context. Considering that ToM is strongly interlinked with language development (Astington & Baird, 2005) and involves action representations, a potential link between compromised frontotemporal (action-perception) circuits and ToM abnormalities is of high interest. To spell out this connection more specifically, it might be advantageous to consider the picture story in Fig. 4. In this case, the observed action that person A put a bug in the bag contrasts with the assumption that the person handing over a present is delivering something nice. One reason for failure in the ToM task may be because these actions were not appropriately processed, memorized or evaluated in the context of the scene. Such a deficit in representing and processing actions, as it is implicated by an action perception integration problem, would certainly complicate performance on this type of task, although a ToM deficit independent of action content and other factors could also contribute to failure.

Fig. 4 — One of several stories in a Theory of Mind task developed and made freely available by Brüne (2003). In this story, the critical questions are a) what person B, in the blue shirt, believes is in the bag (false belief); b) what person B believes that person A, in the red shirt, intends to do (second order false belief); and c) what person A believes that person B believes that they, person A, intend to do (third order false belief). Several potential actions have to be processed and represented in a scenario like this. In this case, the observed action (putting a bug in the bag) contrasts with person B's assumption that person A will be giving them a present.

Functional (Yang, Rosenblau, Keifer, & Pelphrey, 2015) and anatomical (Herbet et al., 2014) data suggest there are multiple routes to understanding other minds and multiple systems which typically interact in doing so — an interaction which is conspicuously atypical in autism (Fishman, Keown, Lincoln, Pineda, & Müller, 2014). These interacting systems include 'higher-order' mentalizing areas (ventromedial prefrontal cortex, cingulate cortex and temporoparietal junction) *and* 'lower-order' simulatory areas (premotor and somatosensory cortex, the frontoparietal mirror network) (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Herbet et al., 2014; Keysers & Gazzola, 2007; Lombardo, Chakrabarti, Bullmore, Wheelwright, et al., 2010; Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010; Sperduti, Guionnet, Fossati, & Nadel, 2014; Spunt & Lieberman, 2012; Zaki, Weber, Bolger, & Ochsner, 2009). As mirror neuron theorists have differentiated between shallow recognition of actions and "understanding from the inside" through action simulation (Rizzolatti & Sinigaglia, 2010), so too have scientists studying mentalizing and social cognition differentiated between the onerous, flexible and potentially conscious "Type 2" processes associated with mentalizing regions and the automatic, stimulus-driven and effortless "Type 1" embodied processing (Bohl & van den Bos, 2012). The embodied route might take the form of "using oneself as a proxy for

understanding others" (Lombardo & Baron-Cohen, 2011, p. 134), where simulation of "embodied" information gives us privileged, fast, phenomenological access to the experience of others. These Type 1 processes might also be analogous to the typical usage of what Mostofsky and Ewen (2011) describe as 'internal action models' stored in the same simulatory areas as mentioned above (the premotor-parietal mirror circuit): conglomerations of motor plans and associated sensory feedback which might be employed via feed-forward mechanisms to aid intention understanding.

From previous research, we know that sensorimotor systems have causal influences on emotion recognition (see Section 7), that observing the movement of others affords information on their emotional states (Hubert et al., 2007; Patel et al., 2012), beliefs (Grèzes, Frith, & Passingham, 2004) and social intent (Becchio, Sartori, Bulgheroni, & Castiello, 2008a, 2008b; Georgiou, Becchio, Glover, & Castiello, 2007; Sartori, Becchio, Bara, & Castiello, 2009), and that the same frontoparietal 'mirror' systems which respond to action execution and observation, along with the insula, also activate while perceiving faces indicating psychological states of others (Di Cesare et al., 2015). Dysfunction and connectivity within and between motor systems and other cortical regions would affect the interaction between the higher-order and lower-order systems involved in mentalizing. Movement-

impaired people with ASC (and indeed other movement-impaired children with ToM deficits [Caillies, Hody, & Calmus, 2012]) may therefore be forced to be "disembodied 'theorists'" (Lombardo & Baron-Cohen, 2011, p. 134), lacking clues from motor systems and that simulative insight from the inside (Rizzolatti & Fabbri-Destro, 2010; Rizzolatti, Fabbri-Destro, & Cattaneo, 2009). Similarly, Mostofsky and Ewen (2011) posit that autistic symptomatology goes back to deficiencies in the aforementioned internal action models, and offer an explanatory pathway from action perception integration to 'embodied' mentalizing.

How the precise interplay between these systems gives rise to complex mentalizing is the focus of ongoing research attention. One interesting avenue for investigation concerns the finding that higher-order mentalizing regions are involved in understanding sentences where an expected outcome is negated (Grisoni et al., 2017). In many ToM tasks, different 'possible worlds' (outcomes involving action sequences) must be evaluated against each other with at least one possibility being finally discarded; could the co-occurring and interactive activations of sensorimotor and mentalizing areas in mentalizing tasks relate to the processing and discarding of action sequences?

In so far as ASC are concerned, differences in motor systems and frontoparietal mirror systems have been described above, but problematically these individuals also show differences in the function of Type 2 mentalizing areas (Lombardo, Chakrabarti, Bullmore, & Baron-Cohen, 2011; Lombardo, Chakrabarti, Bullmore, Sadek et al., 2010). Therefore, the compensatory mechanisms that autistic people use during mentalizing, not to mention their anecdotal cost in terms of stress and energy (Baldwin & Costley, 2016; Bargiela, Steward, & Mandy, 2016; Hendrickx, 2015), are of high research interest. Investigations into ToM may, in addition, be further linked with visual perspective-taking, which has been proposed to rely on some of the same neural substrates as mental perspective-taking (Buckner & Carroll, 2007; Hamilton, Brindley, & Frith, 2009; Spreng & Grady, 2010; Spreng, Mar, & Kim, 2009). A preliminary study with a very small sample links improving physical 'motor' perspective taking (facilitating an actor performing a physical action) with increased language of mental states and mental perspective-taking (Studenka, Gillam, Hartzheim, & Gillam, 2017). The ability to mentally 'put yourself in another's place', to simulate their visual perspective, is known to be challenging for individuals with ASC (Conson et al., 2015; Pearson, Ropar, & Hamilton, 2013) and is suggested, like mentalizing, to rely on alternative processing strategies. Investigation of the neural mechanisms of these strategies is of high research importance.

Another area where motor systems may play a critical role in socio-communicative function is in pragmatics, an area of immense difficulty for people with ASC (Eigsti et al., 2011). Neurometabolic and neurophysiological studies have demonstrated that the motor system may be crucially involved in embedding words and sentences, the structural 'bones' of language, in the functional 'flesh' of communicative speech acts (Egorova, Pulvermüller, & Shtyrov, 2014; Egorova, Shtyrov, & Pulvermüller, 2013, 2016): For example, if the same utterances are used for naming objects, premotor cortex will not be recruited, but when the same words are used for the speech act of requesting (or asking for) an object, motor system recruitment is prominent. At present we largely lack evidence addressing the brain mechanisms of pragmatic language understanding in social-communicative interaction. However, as interactive communication is a notorious problem for individuals with autism, we might hypothesise that neuropragmatic activity, and hence the neural differentiation between different types of speech acts, may be less clear than in TD individuals. Early research in this area has indeed demonstrated differences in brain activity linked to pragmatic understanding (Tesink et al., 2009). Better understanding the neural basis of pragmatics, and the profound difficulties that autistic people experience in communication, beyond the understanding of linguistic structures and the mechanics of using speech, will be an important research goal for the future.

9. Summary, conclusions and future directions

In light of the above, focus on autistic motor disorder and the role of motor systems in higher cognition may have important clinical and therapeutic implications which are now beginning to be explored (Donnellan et al., 2013; Lee, Lambert, Wittich, & Park, 2016; McCleery et al., 2013). We suggest, in closing, that the aforementioned 'broken mirrors' hypothesis of autism may have been a straw man which, however, has pointed the way to fruitful research in autism. There are reports of abnormalities in mirror neuron function (see Section 3) but if one argues that ASC is the result of absent or universally and globally 'broken' mirror neurons this may be considered falsified by instances where 'motor resonance' or activity in mirror neuron regions is indeed present (Becchio & Castiello, 2012; Enticott et al., 2013; Oberman et al., 2008). It cannot, however, be denied that motor systems, which contain mirror neurons, are categorically dysfunctional or functionally atypical in ASC, as we observe in studying higher cognitive skills, for example in action semantic processing; and that, in accordance with the grounding of 'higher' processes in sensorimotor systems, such differences will have marked effects on development. We suggest a wealth of motoric, perceptual and cognitive features of ASC may be understood in terms of a deficit in action perception integration which may relate to aberrant development of long-distance fibre tracts, especially those corticocortical tracts linking anterior to posterior regions.

Our goal in this article was certainly not to explain the whole autistic phenotype via motor dysfunction alone; a local motor cortex (or mirror neuron) abnormality does not provide sufficient explanatory power for these complex conditions. As noted in Section 2, movement impairments are shared by several neurodevelopmental conditions (Gillberg, 2010), where they would be equally expected to impair development in other domains (see Leonard & Hill, 2014). Findings related to the behavioural differences between autism and developmental conditions are patchy and inconsistent (Section 2), relating only to children. We focused in this review on ASC, given the preponderance of data concerning the neural substrates of motor disorder and dysconnectivity within and between cortical motor systems, but it is likely that the neural

substrates of motor dysfunction in conditions such as DCD, SLI and ADHD differ from those seen in autism. It thus remains to ascertain the precise nature of early motor disorder in these developmental conditions, how it differs from that of ASC at the behavioural and the neural level, such that we may understand emergent differences in the phenotypes. As such, an important research goal would be to longitudinally track and compare motor impairments and related cognitive and social development in not only ASC but other developmental conditions marked by early motor deficits and to attempt to further differentiate the neural (and genetic) configurations (including extent of motor [and non-motor] disruption) which set these conditions apart. Given the existence of subtypes within these conditions, a worthy goal might be to analyse brain differences between participants grouped by their deficits, rather than their diagnoses.

Our goal in this article was to illuminate the relationship between motor dysfunction and features that are cardinal to the autistic phenotype but which may appear to some extent (an extent likely related to the precise neural substrates underlying motor dysfunction) in other conditions. These features are language delay or disruption; deficits in action semantics and highly abstract emotion concepts, which could extend beyond word and action-related language processing to problems with imitation, gesture, action recognition and understanding; social cognition, motivation and crucially to social-communicative interaction and pragmatic language understanding; mentalizing and impairment in understanding intentions and emotions, alongside emotion words. The aberrant connectivity reflected in poor integration of motor and perceptual information in movement tasks (see Sections 2 and 3) had a parallel in the information mixing deficit seen in our studies in the language and semantic domains: the atypical 'embodiment' of sensorimotor and emotional associations of words. We have suggested, above, a number of areas worthy of investigation where motor disruption and impaired connectivity between motor and non-motor regions could impact on higher cognitive processing.

The proposition that autistic symptoms might have roots in motor dysfunction has been made before in slightly different guises, by authors who have linked motor deficits to a range of cognitive and social impairments (Bo et al., 2016; Donnellan et al., 2013; Klin et al., 2003; Leary & Hill, 1996; McCleery et al., 2013; Mostofsky & Ewen, 2011; Rizzolatti & Fabbri-Destro, 2010) — and so in part we attempt here to build upon and extend this action perception deficit perspective and its neurocognitive consequences. Klin et al. (2003) emphasised the grounding of social and cognitive processes in sensorimotor experience and suggested that this differed in autism, but did not strongly highlight the neurobiological architecture necessary for this 'grounding' or 'embodiment', nor base their account on neurobiological evidence from ASC. A putative neurobiological substrate for embodied cognition and autistic symptoms was introduced in the original 'broken mirrors' hypothesis (Ramachandran & Oberman, 2006), which was later expanded by Rizzolatti and Fabbri-Destro (2010); these authors speak of impairments to mirror neuron systems, implying dysfunction of the link between perception and action. Mostofsky and Ewen (2011) characterize the core abnormality of ASC as an impairment in 'internal action models', reliant on

sensorimotor circuits across posterior parietal and premotor regions for storage and sequencing, which they suggest play functional roles in intention-understanding, praxis, imitation and social communication — thus resulting in deficits in these domains in autism. Eigsti (2013) queries whether the decreased signal-to-noise ratio in ASC results in looser coupling between stimuli and motor actions, thus also pointing toward the explanation of cognitive impairments, especially in facial mimicry. McCleery et al. (2013), in discussing 'motor resonance' (mirror systems) and linking such activity to imitation, language development and aspects of social cognition such as empathy and intention understanding, review interventions which attempt to alleviate developmental difficulties in the aforementioned domains through movement-based interventions (such as, for example, auditory motor mapping training). Although these authors less directly link cognitive and social impairments to disruption of motor systems, their focus on movement interventions in early life as a means of *preventing or improving* these impairments is highly suggestive of a causal role of motor disorder in giving rise to social and cognitive impairments. Finally, whilst stopping short of attributing motor symptoms causal primary to cognitive and social deficits and avoiding identifying neural substrates for any of this symptomatology, Donnellan et al. (2013) revisit some of Leary and Hill's (1996) original ideas in emphasising how destructive motor and sensory symptoms of autism are to the ability of autistic people to communicate and relate to others.

Our current proposal relates to and partially overlaps with these earlier ones. We expand the action perception perspective on autism in particular towards the dimension of comprehension, language processing and meaningful symbol understanding. Most importantly, we tried to take steps toward a neuromechanistic model of ASC, also highlighting key long-range corticocortical connections such as the AF that show a degree of abnormality in this family of syndromes and which may be crucial for action perception integration. More generally, our model proposes a) that action mechanisms normally become linked with perception mechanisms through associative learning and that this link requires a neural basis in the AF and perhaps other fronto-posterior fibre tracts; b) that the neuronal circuits linking action and perceptual information serve as carriers of cognitive functions, including language and communication, and are consequently functionally relevant for understanding and many important aspects of higher cognition, such as abstract emotion processing. These action perception circuits, which are analogous to Mostofsky and Ewen's (2011) 'internal action models', provide a mechanism for 'mirroring' (i.e., the mapping of perceptions to actions) along with a wider range of social and cognitive skills, among which we here particularly highlighted linguistic processing and abstract semantic understanding. We concur with the aforementioned authors (Mostofsky & Ewen, 2011; Rizzolatti & Fabbri-Destro, 2010) that a dysfunction of motor systems *and* of connectivity, including the links between motor (and adjacent prefrontal areas) and perceptual and multimodal posterior areas (especially temporal cortex), would give rise to the looser coupling between perceptual and action-related representations (Eigsti, 2013) and may explain some key features of the motor and cognitive symptoms that characterise ASC.

Whilst some of these previous accounts link deficits described loosely as 'embodied' to mirror neurons (Eigsti, 2013; McCleery et al., 2013; Mostofsky & Ewen, 2011), we expand this perspective through our consideration of how these multimodal cells acquire their properties through information mixing. The existence of mirror neurons itself requires a neurobiological explanation which might be cast in terms of action perception links. We do not postulate a complete absence or complete dysfunction of mirror neurons in ASC (as in the original broken mirrors account) but rather a reduced probability of linkage between frontotemporal action and perception regions (consistent with the deficits we observed in the AF in adults with autism) which would reduce the multimodal properties of these cells. This would consequently disrupt the formation of action perception circuits supporting action, spoken language in general and action semantics in particular — which is consistent with broader abnormality in the whole motor system (and its connections with other cortical regions), rather than focussing on one type of cell, mirror neurons, within this system. This, we suggest, may help explain some (but not all) crucial features of ASC, including motor (from clumsiness to imitation deficits), linguistic (production and understanding), as well as action semantic and cognitive deficits, which can be as specific as those demonstrated for action and abstract emotion words. This approach provides a functional mechanistic link between the elementary motor deficits known to characterise ASC and their most abstract-cognitive dysfunctions in the semantic domain, which was not provided by these previous accounts.

We have highlighted, above, several areas where clarification is needed by future research. Fundamentally, as we have suggested that action perception circuits fail to develop and cells fail to develop their multimodal properties in ASC, it remains to ascertain *why* this is so. Decreased signal-to-noise ratios have been proposed (Eigsti, 2013), but this explanation itself requires explaining at the genetic and brain level, and requires linkage to these behavioural symptoms. Our own studies evince a difference in the adult state of these circuits, but the failure of action perception circuits to develop, and the linkage of this failure with subsequent social and cognitive impairments, requires study from a longitudinal perspective and might best be operationalised through following HR siblings (a subset of whom will inevitably be diagnosed with ASC themselves) and non-HR infants. Hazlett et al. (2017) recently reported that babies at high risk of ASC show especially speeded brain growth already within the first years of life, and that this hypertrophy is associated with the emergence of autistic symptomatology. Although it is not fully clear which deep brain structures are particularly important for this hypertrophy, abnormalities in grey matter are believed to affect the development of cortico-cortical connections: increased gyrification, found in adults with autism, was suggested by one study to precede and give rise to abnormalities in white matter tracts (Ecker et al., 2016). This tentative suggestion could be directly addressed in subsequent work relating brain growth to connectivity changes in infancy.

The exact role and contribution of sensorimotor systems in social and cognitive processes which have been discussed in this article — such as their necessity in understanding action- and emotion-related language (Moseley, Mohr et al., 2013; Moseley,

Pulvermüller, et al., 2013; Moseley, Shtyrov et al., 2015; Moseley, Ypma et al., 2015), and social processes of particular interest in autism, such as pragmatics, perspective-taking, ToM (mentalizing) and social orientation — remain to be elucidated. Likewise, the alternate routes that people with autism may employ for these processes are an important avenue for future research. Many of these processes can be studied in adulthood, but the conclusions we may make are extrapolations, which may not be equivalent with the atypically developing autistic brain. Likewise, neuroimaging *in vivo* can demonstrate alternative, 'disembodied' routes of processing, just as our studies showed a snapshot of the different brain activity seen in autistic adults during semantic processing (Moseley, Mohr et al., 2013; Moseley, Pulvermüller, et al., 2013; Moseley et al., 2014; Moseley, Shtyrov et al., 2015; Moseley, Ypma et al., 2015), but do not inform the developmental trajectory that led to these adult states, or how these states relate to other autistic symptomatology. Longitudinal study of these developmental trajectories might also serve to highlight, as mentioned above, differences in early motor symptoms or the combination of motor and other symptoms which mark out autistic children from those with other neurodevelopmental conditions.

If we conclude that motor systems and their connections to other parts of the brain are essential for higher cognition, then early disruption will 'derail' (Klin et al., 2003) ongoing development of co-dependent cognitive processes. In continuing to explore and ascertain to what degree early motor dysfunction could be causal to or exacerbate impairments in cognition and social processes, it is hoped that the most important future question will become clearer: whether attending therapeutically to early signs of central nervous system abnormality as they emerge in motor dysfunction (prior to diagnosis) can alleviate downstream sociocognitive deficits.

Declaration of interests

The authors report no actual or potential conflicts of interest related to this work.

Funding

Acknowledgements

Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.cortex.2017.11.019.

REFERENCES

Abu-Dahab, S. M. N., Skidmore, E. R., Holm, M. B., Rogers, J. C., & Minshew, N. J. (2013). Motor and tactile-perceptual skill differences between individuals with high-functioning autism and typically developing individuals ages 5-21. *Journal of Autism and Developmental Disorders, 43*(10), 2241–2248. https://doi.org/10.1007/s10803-011-1439-y.

Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In *Current perspectives in dysphasia* (pp. 32–60). Retrieved from: http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Distributed+memory+,+modular+subsystems+and+dysphasia#0.

Ament, K., Mejia, A., Buhlman, R., Erklin, S., Caffo, B., Mostofsky, S., et al. (2015). Evidence for specificity of motor impairments in catching and balance in children with autism. *Journal of Autism and Developmental Disorders, 45*(3), 742–751. https://doi.org/10.1007/s10803-014-2229-0.

American Psychiatric Association. (2000). *Diagnostic and statistical manual of mental disorders (4th edition text revision)*. Washington, DC: American Psychiatric Association.

American Psychiatric Association. (2013). *Diagnostic and statistical manual of mental disorders* (5th ed.) Arlington http://doi.org/10.1176/appi.books.9780890425596.744053.

Amoruso, L., Gelormini, C., Aboitiz, F., Alvarez González, M., Manes, F., Cardona, J. F., et al. (2013). N400 ERPs for actions: Building meaning in context. *Frontiers in Human Neuroscience, 7*, 57. https://doi.org/10.3389/fnhum.2013.00057.

Anderson, M. L. (2003). Embodied cognition: A field guide. *Artificial Intelligence.* https://doi.org/10.1016/S0004-3702(03)00054–7.

Anderson, M. L. (2010). Neural reuse: A fundamental organizational principle of the brain. *The Behavioral and Brain Sciences, 33*(4), 245–266. https://doi.org/10.1017/S0140525X10000853.

Anzulewicz, A., Sobota, K., & Delafield-Butt, J. T. (2016). Toward the Autism Motor Signature: Gesture patterns during smart tablet gameplay identify children with autism. *Scientific Reports, 6*, 1–13. https://doi.org/10.1038/srep31107.

Asonitou, K., Koutsouki, D., Kourtessis, T., & Charitou, S. (2012). Motor and cognitive performance differences between children with and without developmental coordination disorder (DCD). *Research in Developmental Disabilities, 33*(4), 996–1005. https://doi.org/10.1016/j.ridd.2012.01.008.

Asperger, H. (1944). Die "autistischen psychopathen" im kindesalter. *European Archives of Psychiatry and Clinical Neuroscience, 117*(1), 76–136.

Astington, J. W., & Baird, J. A. (2005). Introduction: Why language matters. In *Why language matters for theory of mind* (pp. 3–25). https://doi.org/10.1093/acprof:oso/9780195159912.003.0001.

Aziz-Zadeh, L., & Damasio, A. (2008). Embodied semantics for actions: Findings from functional brain imaging. *Journal of Physiology Paris, 102*, 35–39. https://doi.org/10.1016/j.jphysparis.2008.03.012.

Bak, T. H., & Chandran, S. (2012). What wires together dies together: Verbs, actions and neurodegeneration in motor neuron disease. *Cortex, 48*, 936–944. https://doi.org/10.1016/j.cortex.2011.07.008.

Baldwin, D. A. (1995). Understanding the link between joint attention and language. In *Joint Attention: Its origins and role in development* (pp. 131–158). https://doi.org/10.2307/302397.

Baldwin, S., & Costley, D. (2016). The experiences and needs of female adults with high-functioning autism spectrum disorder. *Autism, 20*(4), 483–495.

Bar-Haim, Y., & Bart, O. (2006). Motor function and social participation in Kindergarten children. *Social Development, 15*(2), 296–310. https://doi.org/10.1111/j.1467-9507.2006.00342.x.

Baranek, G. T. (1999). Autism during infancy: A retrospective video analysis of sensory-motor and social behaviors at 9-12 months of age. *Journal of Autism and Developmental Disorders, 29*(3), 213–224. https://doi.org/10.1023/A:1023080005650.

Barbeau, E. B., Meilleur, A. A. S., Zeffiro, T. A., & Mottron, L. (2015). Comparing motor skills in autism spectrum individuals with and without speech delay. *Autism Research, 8*(6), 682–693. https://doi.org/10.1002/aur.1483.

Bargiela, S., Steward, R., & Mandy, W. (2016). The experiences of late-diagnosed women with autism spectrum conditions: An investigation of the female autism phenotype. *Journal of Autism and Developmental Disorders, 46*(10), 3281–3294.

Baron-Cohen, S. (2000). Is asperger syndrome/high-functioning autism necessarily a disability? *Development and Psychopathology, 12*(3), 489–500. https://doi.org/10.1017/S0954579400003126.

Baron-Cohen, S. (2009). Autism: The empathizing-systemizing (E-S) theory. *Annals of the New York Academy of Sciences, 1156*, 68–80. https://doi.org/10.1111/j.1749-6632.2009.04467.x.

Baron-Cohen, S., Ring, H., Moriarty, J., Schmitz, B., Costa, D., & Ell, P. (1994). Recognition of mental state terms. Clinical findings in children with autism and a functional neuroimaging study of normal adults. *British Journal of Psychiatry, 165*, 640–649.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*, 5–17. https://doi.org/10.1023/A:1005653411471.

Barrós-Loscertales, A., González, J., Pulvermüller, F., Ventura-Campos, N., Bustamante, J. C., Costumero, V., et al. (2012). Reading salt activates gustatory brain regions: FMRI evidence for semantic grounding in a novel sensory modality. *Cerebral Cortex, 22*, 2554–2563. https://doi.org/10.1093/cercor/bhr324.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*(4), 577–660. https://doi.org/10.1017/S0140525X99002149.

Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology, 59*, 617–645. https://doi.org/10.1146/annurev.psych.59.103006.093639.

Barsalou, L. W. (2010). Grounded cognition: Past, present, and future. *Topics in Cognitive Science, 2*(4), 716–724. https://doi.org/10.1111/j.1756-8765.2010.01115.x.

Barttfeld, P., Amoruso, L., Ais, J., Cukier, S., Bavassi, L., Tomio, A., et al. (2013). Organization of brain networks governed by long-

range connections index autistic traits in the general population. *Journal of Neurodevelopmental Disorders, 5*(16), 1–9. https://doi.org/10.1186/1866-1955-5-16.

Bastiaansen, J. A. C. J., Thioux, M., & Keysers, C. (2009). Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society B-Biological Sciences-Biological Sciences, 364*(1528), 2391–2404. https://doi.org/10.1098/rstb.2009.0058.

Bates, E., & Dick, F. (2002). Language, gesture, and the developing brain. *Developmental Psychobiology, 40*(3), 293–310. https://doi.org/10.1002/dev.10034.

Baumeister, J. C., Papa, G., & Foroni, F. (2016). Deeper than skin deep—The effect of botulinum toxin-A on emotion processing. *Toxicon, 118*, 86–90.

Becchio, C., & Castiello, U. (2012). Visuomotor resonance in autism spectrum disorders. *Frontiers in Integrative Neuroscience, 6*, 110. https://doi.org/10.3389/fnint.2012.00110.

Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008a). Both your intention and mine are reflected in the kinematics of my reach-to-grasp movement. *Cognition, 106*(2), 894–912. https://doi.org/10.1016/j.cognition.2007.05.004.

Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008b). The case of Dr. Jekyll and Mr. Hyde: A kinematic study on social intention. *Consciousness and Cognition, 17*(3), 557–564. https://doi.org/10.1016/j.concog.2007.03.003.

Bedford, R., Jones, E. J. H., Johnson, M. H., Pickles, A., Charman, T., & Gliga, T. (2016). Sex differences in the association between infant markers and later autistic traits. *Molecular Autism, 7*(1), 21. https://doi.org/10.1186/s13229-016-0081-0.

Behere, A., Shahani, L., Noggle, C. A., & Dean, R. (2012). Motor functioning in autistic spectrum disorders: A preliminary analysis. *The Journal of Neuropsychiatry and Clinical Neurosciences, 24*(1), 87–94. https://doi.org/10.1176/appi.neuropsych.11050105.

Belmonte, M. K., Cook, E. H., Anderson, G. M., Rubenstein, J. L. R., Greenough, W. T., Beckel-Mitchener, A., et al. (2004). Autism as a disorder of neural information processing: Directions for research and targets for therapy. *Molecular Psychiatry, 9*(7), 646–663. https://doi.org/10.1038/sj.mp.4001499.

Belmonte, M., Saxena-Chandhok, T., Cherian, R., Muneer, R., George, L., & Karanth, P. (2013). Oral motor deficits in speech-impaired children with Autism. *Frontiers in Integrative Neuroscience, 7*, 47. Retrieved from: http://www.frontiersin.org/Journal/DownloadFile.ashx?pdf=1&FileId=70278&articleId=46434&Version=1&ContentTypeId=58&FileName=ProvisionalPDF.pdf%5Cnhttp://ovidsp.ovid.com/ovidweb.cgi?T=JS&PAGE=reference&D=emed11&NEWS=N&AN=2013362512.

Bernier, R., Dawson, G., Webb, S., & Murias, M. (2007). EEG mu rhythm and imitation impairments in individuals with autism spectrum disorder. *Brain and Cognition, 64*(3), 228–237. https://doi.org/10.1016/j.bandc.2007.03.004.

Bhat, A. N., Galloway, J. C., & Landa, R. J. (2012). Relation between early motor delay and later communication delay in infants at risk for autism. *Infant Behavior & Development, 35*(4), 838–846. https://doi.org/10.1016/j.infbeh.2012.07.019.

Bhat, A. N., Landa, R. J., & Galloway, J. C. (2011). Current perspectives on motor functioning in infants, children, and adults with autism spectrum disorders. *Physical Therapy, 91*(7), 1116–1129. https://doi.org/10.2522/ptj.20100294.

Biscaldi, M., Rauh, R., Irion, L., Jung, N. H., Mall, V., Fleischhaker, C., et al. (2014). Deficits in motor abilities and developmental fractionation of imitation performance in high-functioning autism spectrum disorders. *European Child and Adolescent Psychiatry, 23*(7), 599–610. https://doi.org/10.1007/s00787-013-0475-x.

Bo, J., Lee, C.-M., Colbert, A., & Shen, B. (2016). Do children with autism spectrum disorders have motor learning difficulties? *Research in Autism Spectrum Disorders, 23*, 50–62. https://doi.org/10.1016/j.rasd.2015.12.001.

Bohl, V., & van den Bos, W. (2012). Toward an integrative account of social cognition: Marrying theory of mind and interactionism to study the interplay of Type 1 and Type 2 processes. *Frontiers in Human Neuroscience, 6*, 274.

Boulenger, V., Mechtouff, L., Thobois, S., Broussolle, E., Jeannerod, M., & Nazir, T. A. (2008). Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns. *Neuropsychologia, 46*, 743–756. https://doi.org/10.1016/j.neuropsychologia.2007.10.007.

Boulenger, V., Shtyrov, Y., & Pulvermüller, F. (2012). When do you grasp the idea? MEG evidence for instantaneous idiom understanding. *NeuroImage, 59*(4), 3502–3513. https://doi.org/10.1016/j.neuroimage.2011.11.011.

Braadbaart, L., de Grauw, H., Perrett, D. I., Waiter, G. D., & Williams, J. H. G. (2014). The shared neural basis of empathy and facial imitation accuracy. *NeuroImage, 84*, 367–375. https://doi.org/10.1016/j.neuroimage.2013.08.061.

Braitenberg, V., & Schüz, A. (1998). *Cortex: Statistics and geometry of neuronal connectivity. Berlin, Germany: Springer-Verlag.*

Brian, J., Bryson, S. E., Garon, N., Roberts, W., Smith, I. M., Szatmari, P., et al. (2008). Clinical assessment of autism in high-risk 18-month-olds. *Autism, 12*(5), 433–456. https://doi.org/10.1177/1362361308094500.

Brisson, J., Warreyn, P., Serres, J., Foussier, S., & Adrien-Louis, J. (2012). Motor anticipation failure in infants with autism: A retrospective analysis of feeding situations. *Autism, 16*(4), 420–429. https://doi.org/10.1177/1362361311423385.

Brown-Lum, M., & Zwicker, J. G. (2015). Brain imaging increases our understanding of developmental coordination disorder: A review of literature and future directions. *Current Developmental Disorders Reports, 2*(2), 131–140. https://doi.org/10.1007/s40474-015-0046-6.

Brüne, M. (2003). Theory of mind and the role of IQ in chronic disorganized schizophrenia. *Schizophrenia Research, 60*(1), 57–64. https://doi.org/10.1016/S0920-9964(02)00162-7.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11*(2), 49–57. https://doi.org/10.1016/j.tics.2006.11.004.

Caillies, S., Hody, A., & Calmus, A. (2012). Theory of mind and irony comprehension in children with cerebral palsy. *Research in Developmental Disabilities, 33*(5), 1380–1388. https://doi.org/10.1016/j.ridd.2012.03.012.

Campione, G. C., Piazza, C., Villa, L., & Molteni, M. (2016). Three-dimensional kinematic analysis of prehension movements in young children with autism spectrum disorder: New insights on motor impairment. *Journal of Autism and Developmental Disorders, 46*(6), 1985–1999. https://doi.org/10.1007/s10803-016-2732-6.

Campos, J. J., Anderson, D. I., Barbu-Roth, M., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. (2000). Travel broadens the mind. *Infancy, 1*(2), 149–219. https://doi.org/10.1207/S15327078IN0102.

Cardona, J. F., Kargieman, L., Sinay, V., Gershanik, O., Gelormini, C., Amoruso, L., et al. (2014). How embodied is action language? Neurological evidence from motor diseases. *Cognition, 131*(2), 311–322. https://doi.org/10.1016/j.cognition.2014.02.001.

Carota, F., Moseley, R., & Pulvermüller, F. (2012). Body-part-specific representations of semantic noun categories. *Journal of Cognitive Neuroscience, 24*(6), 1492–1509. https://doi.org/10.1162/jocn_a_00219.

Carper, R. A., Solders, S., Treiber, J. M., Fishman, I., & Müller, R. A. (2015). Corticospinal tract anatomy and functional connectivity of primary motor cortex in autism. *Journal of the American Academy of Child and Adolescent Psychiatry, 54*(10), 859–867. https://doi.org/10.1016/j.jaac.2015.07.007.

Casanova, M., & Trippe, J. (2009). Radial cytoarchitecture and patterns of cortical connectivity in autism. *Philosophical*

Transactions of the Royal Society of London. Series B, Biological Sciences, 364, 1433—1436. https://doi.org/10.1098/rstb.2008.0331.

Casartelli, L., Molteni, M., & Ronconi, L. (2016). So close yet so far: Motor anomalies impacting on social functioning in autism spectrum disorder. Neuroscience and Biobehavioral Reviews. https://doi.org/10.1016/j.neubiorev.2016.02.001.

Casasanto, D. (2011). Different bodies, different minds: The body specificity of language and thought. Current Directions in Psychological Science. https://doi.org/10.1177/0963721411422058.

Catani, M., Dell'Acqua, F., Budisavljevic, S., Howells, H., De Schotten, M., Froudist-Walsh, S., et al. (2016). Frontal networks in adults with autism spectrum disorder. Brain, 139(2), 616—630.

Cattaneo, L., Fabbri-Destro, M., Boria, S., Pieraccini, C., Monti, A., Cossu, G., et al. (2007). Impairment of actions chains in autism and its possible role in intention understanding. Proceedings of the National Academy of Sciences of the United States of America, 104(45), 17825—17830. https://doi.org/10.1073/pnas.0706273104.

Centelles, L., Assaiante, C., Nazarian, B., Anton, J. L., & Schmitz, C. (2011). Recruitment of both the mirror and the mentalizing networks when observing social interactions depicted by point-lights: A neuroimaging study. PLoS One, 6(1). https://doi.org/10.1371/journal.pone.0015749.

Chao, L. L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. Journal of Cognitive Neuroscience, 11, 25—35. https://doi.org/10.1162/089892999563229.

Chevallier, C., Kohls, G., Troiani, V., Brodkin, E. S., & Schultz, R. T. (2012). The social motivation theory of autism. Trends in Cognitive Sciences. https://doi.org/10.1016/j.tics.2012.02.007.

Christensen, D. L., Baio, J., Braun, K. V. N., Bilder, D., Charles, J., Constantino, J. N., et al. (2016). Prevalence and characteristics of autism spectrum disorder among children aged 8 years - autism and developmental disabilities monitoring network, 11 sites, United States, 2012. Morbidity and Mortality Weekly Report. Surveillance Summaries (Washington, D.C.: 2002), 65(3), 1—23. https://doi.org/10.15585/mmwr.ss6503a1.

Chukoskie, L., Townsend, J., & Westerfield, M. (2013). Motor skill in autism spectrum disorders: A subcortical view. International Review of Neurobiology, 113, 207—249. https://doi.org/10.1016/B978-0-12-418700-9.00007-1.

Clearfield, M. W. (2011). Learning to walk changes infants' social interactions. Infant Behavior and Development, 34(1), 15—25. https://doi.org/10.1016/j.infbeh.2010.04.008.

Clifford, S. M., & Dissanayake, C. (2008). The early development of joint attention in infants with autistic disorder using home video observations and parental interview. Journal of Autism and Developmental Disorders, 38(5), 791—805. https://doi.org/10.1007/s10803-007-0444-7.

Clifford, S. M., Hudry, K., Elsabbagh, M., Charman, T., & Johnson, M. H. (2013). Temperament in the first 2 years of life in infants at high-risk for autism spectrum disorders. Journal of Autism and Developmental Disorders, 43(3), 673—686. https://doi.org/10.1007/s10803-012-1612-y.

Clifford, S., Young, R., & Williamson, P. (2007). Assessing the early characteristics of autistic disorder using video analysis. Journal of Autism and Developmental Disorders, 37(2), 301—313. https://doi.org/10.1007/s10803-006-0160-8.

Cochet, H., & Byrne, R. W. (2016). Communication in the second and third year of life: Relationships between nonverbal social skills and language. Infant Behavior and Development, 44, 189—198.

Colombo-Dougovito, A. M., & Reeve, R. E. (2017). Exploring the interaction of motor and social skills with autism severity using the SFARI dataset. Perceptual and Motor Skills, 124(2), 413—424. https://doi.org/10.1177/0031512516689198.

Conson, M., Mazzarella, E., Esposito, D., Grossi, D., Marino, N., Massagli, A., et al. (2015). "Put myself into your Place": Embodied simulation and perspective taking in autism spectrum disorders. Autism Research, 8(4), 454—466. https://doi.org/10.1002/aur.1460.

Constantino, J. N., Davis, S. A., Todd, R. D., Schindler, M. K., Gross, M. M., Brophy, S. L., et al. (2003). Validation of a brief quantitative measure of autistic traits: Comparison of the social responsiveness scale with the Autism Diagnostic Interview-Revised. Journal of Autism and Developmental Disorders, 33(4), 427—433. https://doi.org/10.1023/A:1025014929212.

Cook, J. (2016). From movement kinematics to social cognition: The case of autism. Philosophical Transactions of the Royal Society, 8—10. https://doi.org/10.1098/rstb.2015.0372.

Cook, J., Association, A. P., Macintosh, K., Dissanayake, C., Nayate, A., Bradshaw, J., et al. (2016). From movement kinematics to social cognition: The case of autism. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 371(1693), 421—434. https://doi.org/10.1098/rstb.2015.0372.

Cook, J. L., Blakemore, S. J., & Press, C. (2013). Atypical basic movement kinematics in autism spectrum conditions. Brain, 136(9), 2816—2824. https://doi.org/10.1093/brain/awt208.

Cossu, G., Boria, S., Copioli, C., Bracceschi, R., Giuberti, V., Santelli, E., et al. (2012). Motor representation of actions in children with autism. PLoS One, 7(9). https://doi.org/10.1371/journal.pone.0044779.

Cotelli, M., Borroni, B., Manenti, R., Alberici, A., Calabria, M., Agosti, C., et al. (2006). Action and object naming in frontotemporal dementia, progressive supranuclear palsy, and corticobasal degeneration. Neuropsychology, 20, 558—565. https://doi.org/10.1037/0894-4105.20.5.558.

Courchesne, E., & Pierce, K. (2005). Why the frontal cortex in autism might be talking only to itself: Local over-connectivity but long-distance disconnection. Current Opinion in Neurobiology. https://doi.org/10.1016/j.conb.2005.03.001.

Crippa, A., Salvatore, C., Perego, P., Forti, S., Nobile, M., Molteni, M., et al. (2015). Use of machine learning to identify children with autism and their motor abnormalities. Journal of Autism and Developmental Disorders, 45(7), 2146—2156. https://doi.org/10.1007/s10803-015-2379-8.

Cummins, A., Piek, J. P., & Dyck, M. J. (2005). Motor coordination, empathy, and social behaviour in school-aged children. Developmental Medicine and Child Neurology, 47(7), 437—442. https://doi.org/10.1111/j.1469-8749.2005.tb01168.x.

D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The motor somatotopy of speech perception. Current Biology, 19, 381—385. https://doi.org/10.1016/j.cub.2009.01.017.

Dajani, D., & Uddin, L. (2016). Local brain connectivity across development in autism spectrum disorder: A cross-sectional investigation. Autism Research, 9(1), 43—54.

Dalton, J. C., Crais, E. R., & Velleman, S. L. (2017). Joint attention and oromotor abilities in young children with and without autism spectrum disorder. Journal of Communication Disorders, 69, 27—43.

Damasio, A. R., & Maurer, R. G. (1978). A neurological model for childhood autism. Archives of Neurology, 35(12), 777. https://doi.org/10.1001/archneur.1978.00500360001001.

Dapretto, M., Davies, M. S., Pfeifer, J. H., Scott, A. A., Sigman, M., Bookheimer, S. Y., et al. (2006). Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. Nature Neuroscience, 9(1), 28—30. https://doi.org/10.1038/nn1611.

David, F. J., Baranek, G. T., Wiesen, C., Miao, A., & Thorpe, D. E. (2012). Coordination of precision grip in 2—6 years-old children with autism spectrum disorders compared to children

developing typically and children with developmental disabilities. *Frontiers in Integrative Neuroscience, 6*(122).

Dawson, G., Toth, K., Abbott, R., Osterling, J., Munson, J., Estes, A., et al. (2004). Early social attention impairments in autism: Social orienting, joint attention, and attention to distress. *Developmental Psychology, 40*(2), 271–283. https://doi.org/10.1037/0012-1649.40.2.271.

Dawson, G., Warrenburg, S., & Fuller, P. (1983). Hemisphere functioning and motor imitation in autistic persons. *Brain and Cognition, 2*(4), 346–354. https://doi.org/10.1016/0278-2626(83)90018-0.

Decety, J., & Meltzoff, A. N. (2011). Empathy, imitation, and the social brain. *Empathy: Philosophical and Psychological Perspectives,* 58–81.

Dewey, D., Cantell, M., & Crawford, S. G. (2007). Motor and gestural performance in children with autism spectrum disorders, developmental coordination disorder, and/or attention deficit hyperactivity disorder. *Journal of the International Neuropsychological Society: JINS, 13*(2), 246–256. https://doi.org/10.1017/S1355617707070270.

Dewey, D., Kaplan, B. J., Crawford, S. G., & Wilson, B. N. (2002). Developmental coordination disorder: Associated problems in attention, learning, and psychosocial adjustment. *Human Movement Science, 21*(5–6), 905–918. https://doi.org/10.1016/S0167-9457(02)00163-X.

Di Cesare, G., Di Dio, C., Marchi, M., & Rizzolatti, G. (2015). Expressing our internal states and understanding those of others. *Proceedings of the National Academy of Sciences, 112*(33). https://doi.org/10.1073/pnas.1512133112, 201512133.

Di Martino, A., Fair, D. A., Kelly, C., Satterthwaite, T. D., Castellanos, F. X., Thomason, M. E., et al. (2014). Unraveling the miswired connectome: A developmental perspective. *Neuron, 83*(6), 1335–1353. https://doi.org/10.1016/j.neuron.2014.08.050.

Di Martino, A., Kelly, C., Grzadzinski, R., Zuo, X. N., Mennes, M., Mairena, M. A., et al. (2011). Aberrant striatal functional connectivity in children with autism. *Biological Psychiatry, 69*(9), 847–856. https://doi.org/10.1016/j.biopsych.2010.10.029.

Donnellan, A. M., Hill, D. A., & Leary, M. R. (2013). Rethinking autism: Implications of sensory and movement differences for understanding and support. *Frontiers in Integrative Neuroscience, 6*, 124. https://doi.org/10.3389/fnint.2012.00124.

Dowd, A. M., McGinley, J. L., Taffe, J. R., & Rinehart, N. J. (2012). Do planning and visual integration difficulties underpin motor dysfunction in autism? A kinematic study of young children with autism. *Journal of Autism and Developmental Disorders, 42*(8), 1539–1548. https://doi.org/10.1007/s10803-011-1385-8.

Dowell, L. R., Mahone, E. M., & Mostofsky, S. H. (2009). Associations of postural knowledge and basic motor skill with dyspraxia in. *Neuropsychology, 23*(5), 563–570. https://doi.org/10.1037/a0015640.

Downey, R., & Rapport, M. J. K. (2012). Motor activity in children with autism: A review of current literature. *Pediatric Physical Therapy: The Official Publication of the Section on Pediatrics of the American Physical Therapy Association, 24*(1), 2–20. https://doi.org/10.1097/PEP.0b013e31823db95f.

Dreyer, F. R., Frey, D., Arana, S., von Saldern, S., Picht, T., Vajkoczy, P., et al. (2015). Is the motor system necessary for processing action and abstract emotion words? Evidence from focal brain lesions. *Frontiers in Psychology, 6*. https://doi.org/10.3389/fpsyg.2015.01661.

Duffield, T. C., Trontel, H. G., Bigler, E. D., Froehlich, A., Prigge, M. B., Travers, B., et al. (2013). Neuropsychological investigation of motor impairments in autism. *Journal of Clinical and Experimental Neuropsychology, 35*(8), 867–881. https://doi.org/10.1080/13803395.2013.827156.

Dunn, M., Gomes, H., & Sebastian, M. J. (1996). Prototypicality of responses of autistic, language disordered, and normal children in a word fluency task. *Child Neuropsychology*. https://doi.org/10.1080/09297049608401355.

Dyck, M. J., Piek, J. P., Hay, D. A., & Hallmayer, J. F. (2007). The relationship between symptoms and abilities in autism. *Journal of Developmental and Physical Disabilities, 19*(3), 251–261. https://doi.org/10.1007/s10882-007-9055-7.

Dziuk, M. A., Larson, J. C. G., Apostu, A., Mahone, E. M., Denckla, M. B., & Mostofsky, S. H. (2007). Dyspraxia in autism: Association with motor, social, and communicative deficits. *Developmental Medicine and Child Neurology, 49*(10), 734–739. https://doi.org/10.1111/j.1469-8749.2007.00734.x.

Ecker, C., Andrews, D., Dell'Acqua, F., Daly, E., Murphy, C., Catani, M., et al. (2016). Relationship between cortical gyrification, white matter connectivity, and autism spectrum disorder. *Cerebral Cortex, 26*(7), 3297–3309. https://doi.org/10.1093/cercor/bhw098.

Ecker, C., Rocha-Rego, V., Johnston, P., Mourao-Miranda, J., Marquand, A., Daly, E. M., et al. (2010). Investigating the predictive value of whole-brain structural MR scans in autism: A pattern classification approach. *NeuroImage, 49*(1), 44–56. https://doi.org/10.1016/j.neuroimage.2009.08.024.

Efstratopoulou, M., Janssen, R., & Simons, J. (2012). Differentiating children with attention-deficit/hyperactivity disorder, conduct disorder, learning disabilities and autistic spectrum disorders by means of their motor behavior characteristics. *Research in Developmental Disabilities, 33*(1), 196–204. https://doi.org/10.1016/j.ridd.2011.08.033.

Egorova, N., Pulvermüller, F., & Shtyrov, Y. (2014). Neural dynamics of speech act comprehension: An MEG study of naming and requesting. *Brain Topography*. https://doi.org/10.1007/s10548-013-0329-3.

Egorova, N., Shtyrov, Y., & Pulvermüller, F. (2013). Early and parallel processing of pragmatic and semantic information in speech acts: Neurophysiological evidence. *Frontiers in Human Neuroscience, 7*, 86. https://doi.org/10.3389/fnhum.2013.00086.

Egorova, N., Shtyrov, Y., & Pulvermüller, F. (2016). Brain basis of communicative actions in language. *NeuroImage, 125*, 857–867. https://doi.org/10.1016/j.neuroimage.2015.10.055.

Eigsti, I.-M. (2013). A review of embodiment in autism spectrum disorders. *Frontiers in Psychology, 4*, 224. https://doi.org/10.3389/fpsyg.2013.00224.

Eigsti, I. M., De Marchena, A. B., Schuh, J. M., & Kelley, E. (2011). Language acquisition in autism spectrum disorders: A developmental review. *Research in Autism Spectrum Disorders*. https://doi.org/10.1016/j.rasd.2010.09.001.

Eigsti, I. M., Rosset, D., Col Cozzari, G., da Fonseca, D., & Deruelle, C. (2015). Effects of motor action on affective preferences in autism spectrum disorders: Different influences of embodiment. *Developmental Science, 18*(6), 1044–1053. https://doi.org/10.1111/desc.12278.

Einspieler, C., Sigafoos, J., Bartl-Pokorny, K. D., Landa, R., Marschik, P. B., & Bölte, S. (2014). Highlighting the first 5 months of life: General movements in infants later diagnosed with autism spectrum disorder or Rett syndrome. *Research in Autism Spectrum Disorders, 8*(3), 286–291. https://doi.org/10.1016/j.rasd.2013.12.013.

Enticott, P. G., Bradshaw, J. L., Iansek, R., Tonge, B. J., & Rinehart, N. J. (2009). Electrophysiological signs of supplementary-motor-area deficits in high-functioning autism but not Asperger syndrome: An examination of internally cued movement-related potentials. *Developmental Medicine and Child Neurology, 51*(10), 787–791. https://doi.org/10.1111/j.1469-8749.2009.03270.x.

Enticott, P. G., Kennedy, H. A., Rinehart, N. J., Bradshaw, J. L., Tonge, B. J., Daskalakis, Z. J., et al. (2013). Interpersonal motor resonance in autism spectrum disorder: Evidence against a

global "mirror system" deficit. *Frontiers in Human Neuroscience,* 7, 218. https://doi.org/10.3389/fnhum.2013.00218.

Esposito, G., & Paşca, S. P. (2013). Motor abnormalities as a putative endophenotype for autism spectrum disorders. *Frontiers in Integrative Neuroscience, 7,* 43. https://doi.org/10.3389/fnint.2013.00043.

Esposito, G., & Venuti, P. (2008). Analysis of toddlers' gait after six months of independent walking to identify autism: A preliminary study. *Perceptual and Motor Skills, 106*(1), 259–269. https://doi.org/10.2466/pms.106.1.259-269.

Esposito, G., Venuti, P., Maestro, S., & Muratori, F. (2009). An exploration of symmetry in early autism spectrum disorders: Analysis of lying. *Brain and Development, 31*(2), 131–138. https://doi.org/10.1016/j.braindev.2008.04.005.

Fabbri-Destro, M., Cattaneo, L., Boria, S., & Rizzolatti, G. (2009). Planning actions in autism. *Experimental Brain Research, 192,* 521–525. https://doi.org/10.1007/s00221-008-1578-3.

Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology.* https://doi.org/10.1016/j.conb.2005.03.013.

Fair, D., Nigg, J. T., Iyer, S., Bathula, D., Mills, K. L., Dosenbach, N. U. F., et al. (2012). Distinct neural signatures detected for ADHD subtypes after controlling for micro-movements in resting state functional connectivity MRI data. *Frontiers in Systems Neuroscience, 6,* 80. https://doi.org/10.3389/fnsys.2012.00080.

Fargier, R., Paulignan, Y., Boulenger, V., Monaghan, P., Reboul, A., & Nazir, T. A. (2012). Learning to associate novel words with motor actions: Language-induced motor activity following short training. *Cortex, 48,* 888–899. https://doi.org/10.1016/j.cortex.2011.07.003.

Fatemi, S. H., Aldinger, K. A., Ashwood, P., Bauman, M. L., Blaha, C. D., Blatt, G. J., et al. (2012). Consensus paper: Pathological role of the cerebellum in Autism. *The Cerebellum.* https://doi.org/10.1007/s12311-012-0355-9.

Fischer, M. H., & Zwaan, R. A. (2008). Embodied language-A review of the role of the motor system in language comprehension. *Quarterly Journal of Experimental Psychology, 61,* 825–850.

Fishman, I., Keown, C. L., Lincoln, A. J., Pineda, J. a, & Müller, R.-A. (2014). Atypical cross talk between mentalizing and mirror neuron networks in autism spectrum disorder. *JAMA Psychiatry, 71*(7), 751–760. https://doi.org/10.1001/jamapsychiatry.2014.83.

Flanagan, J. E., Landa, R., Bhat, A., & Bauman, M. (2012). Head lag in infants at risk for autism: A preliminary study. *American Journal of Occupational Therapy, 66*(5), 577–585. https://doi.org/10.5014/ajot.2012.004192.

Floris, D. L., Barber, A. D., Nebel, M. B., Martinelli, M., Lai, M.-C., Crocetti, D., et al. (2016). Atypical lateralization of motor circuit functional connectivity in children with autism is associated with motor deficits. *Molecular Autism, 7*(1), 35. https://doi.org/10.1186/s13229-016-0096-6.

Fodor, J. A., & Pylyshyn, Z. W. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition, 28*(1–2), 3–71. https://doi.org/10.1016/0010-0277(88)90031-5.

Fournier, K. A., Hass, C. J., Naik, S. K., Lodha, N., & Cauraugh, J. H. (2010). Motor coordination in autism spectrum disorders: A synthesis and meta-analysis. *Journal of Autism and Developmental Disorders, 40,* 1227–1240. https://doi.org/10.1007/s10803-010-0981-3.

Fox, M. D., & Raichle, M. E. (2007). Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nature Reviews. Neuroscience, 8*(9), 700–711. https://doi.org/10.1038/nrn2201.

Frazier, T. W., Youngstrom, E. A., Speer, L., Embacher, R., Law, P., Constantino, J., et al. (2012). Validation of proposed DSM-5 criteria for autism spectrum disorder. *Journal of the American Academy of Child and Adolescent Psychiatry, 51*(1). https://doi.org/10.1016/j.jaac.2011.09.021.

Freitag, C. M., Konrad, C., Häberlen, M., Kleser, C., von Gontard, A., Reith, W., et al. (2008). Perception of biological motion in autism spectrum disorders. *Neuropsychologia, 46*(5), 1480–1494. https://doi.org/10.1016/j.neuropsychologia.2007.12.025.

Friedmann, N., & Novogrodsky, R. (2008). Subtypes of SLI: SySLI, PhoSLI, LeSLI, and PraSLI. *Language Acquisition and Development,* 205–217.

Friedmann, N., & Novogrodsky, R. (2011). Which questions are most difficult to understand? The comprehension of Wh questions in three subtypes of SLI. *Lingua, 121*(3), 367–382. https://doi.org/10.1016/j.lingua.2010.10.004.

Frith, U., & Snowling, M. (1983). Reading for meaning and reading for sound in autistic and dyslexic children. *British Journal of Developmental Psychology, 1*(4), 329–342. https://doi.org/10.1111/j.2044-835X.1983.tb00906.x.

Fuster, J. (2003). *Cortex and mind: Unifying cognition.* Oxford, UK: Oxford University Press.

Gaffrey, M. S., Kleinhans, N. M., Haist, F., Akshoomoff, N., Campbell, A., Courchesne, E., et al. (2007). A typical participation of visual cortex during word processing in autism: An fMRI study of semantic decision. *Neuropsychologia, 45,* 1672–1684. https://doi.org/10.1016/j.neuropsychologia.2007.01.008.

Gallese, V., Gernsbacher, M. a, Heyes, C., Hickok, G., & Iacoboni, M. (2011). Mirror neuron forum. *Perspectives on Psychological Science, 6*(4), 369–407. https://doi.org/10.1177/1745691611413392.

Gallese, V., & Lakoff, G. (2005). The Brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology, 22,* 455–479. https://doi.org/10.1080/02643290442000310.

Garagnani, M., & Pulvermüller, F. (2016). Conceptual grounding of language in action and perception: A neurocomputational model of the emergence of category specificity and semantic hubs. *European Journal of Neuroscience, 43*(6), 721–737. https://doi.org/10.1111/ejn.13145.

Garagnani, M., Wennekers, T., & Pulvermüller, F. (2008). A neuroanatomically grounded Hebbian-learning model of attention-language interactions in the human brain. *European Journal of Neuroscience, 27*(2), 492–513. https://doi.org/10.1111/j.1460-9568.2008.06015.x.

Garagnani, M., Wennekers, T., & Pulvermüller, F. (2009). Recruitment and consolidation of cell assemblies for words by way of hebbian learning and competition in a multi-layer neural network. *Cognitive Computation, 1,* 160–176. https://doi.org/10.1007/s12559-009-9011-1.

García, A., & Ibáñez, A. (2014). Words in motion: Motor-language coupling in Parkinson's disease. *Translational Neuroscience, 5*(2), 152–159. https://doi.org/10.2478/s13380-014-0218-6.

Georgiou, I., Becchio, C., Glover, S., & Castiello, U. (2007). Different action patterns for cooperative and competitive behaviour. *Cognition, 102*(3), 415–433. https://doi.org/10.1016/j.cognition.2006.01.008.

Gernsbacher, M. A., Sauer, E. A., Geye, H. M., Schweigert, E. K., & Hill Goldsmith, H. (2008). Infant and toddler oral- and manual-motor skills predict later speech fluency in autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines, 49,* 43–50. https://doi.org/10.1111/j.1469-7610.2007.01820.x.

Geschwind, D. H., & Levitt, P. (2007). Autism spectrum disorders: Developmental disconnection syndromes. *Current Opinion in Neurobiology.* https://doi.org/10.1016/j.conb.2007.01.009.

Ghaziuddin, M., & Butler, E. (1998). Clumsiness in autism and Asperger syndrome: a further report. 42, 43–48.

Giese, M. A., & Rizzolatti, G. (2015). Neural and computational mechanisms of action processing: Interaction between visual and motor representations. *Neuron.* https://doi.org/10.1016/j.neuron.2015.09.040.

Giles, D. C. (2014). "DSM-V is taking away our identity": The reaction of the online community to the proposed changes in the diagnosis of Asperger's disorder. *Health: An Interdisciplinary Journal for the Social Study of Health, Illness and Medicine, 18*(2), 179−195. https://doi.org/10.1177/1363459313488006.

Gillberg, C. (2010). The ESSENCE in child psychiatry: Early Symptomatic Syndromes Eliciting Neurodevelopmental Clinical Examinations. *Research in Developmental Disabilities, 31*(6), 1543−1551. https://doi.org/10.1016/j.ridd.2010.06.002.

Glenberg, A. M., Havas, D., Becker, R., & Rinck, M. (2005). Grounding language in bodily states: The case for emotion. In *The grounding of cognition: The role of perception and action in memory, language, and thinking* (pp. 1−17).

Glenberg, A. M., & Kaschak, M. P. (2003). The body's contribution to language. *Psychology of Learning and Motivation − Advances in Research and Theory, 43*, 93−126. https://doi.org/10.1016/S0079-7421(03)01012-0.

Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006). Perceptual knowledge retrieval activates sensory brain regions. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 26*, 4917−4921. https://doi.org/10.1523/JNEUROSCI.5389-05.2006.

Goldman, A. I., & Sripada, C. S. (2005). Simulationist models of face-based emotion recognition. *Cognition.* https://doi.org/10.1016/j.cognition.2004.01.005.

Gomez, A., & Sirigu, A. (2015). Developmental coordination disorder: Core sensori-motor deficits, neurobiology and etiology. *Neuropsychologia, 79*, 272−287. https://doi.org/10.1016/j.neuropsychologia.2015.09.032.

Gonzalez-Gadea, M. L., Baez, S., Torralva, T., Castellanos, F. X., Rattazzi, A., Bein, V., et al. (2013). Cognitive variability in adults with ADHD and AS: Disentangling the roles of executive functions and social cognition. *Research in Developmental Disabilities, 34*(2), 817−830. https://doi.org/10.1016/j.ridd.2012.11.009.

González, J., Barros-Loscertales, A., Pulvermüller, F., Meseguer, V., Sanjuán, A., Belloch, V., et al. (2006). Reading cinnamon activates olfactory brain regions. *NeuroImage, 32*, 906−912. https://doi.org/10.1016/j.neuroimage.2006.03.037.

Gowen, E., & Hamilton, A. (2013). Motor abilities in autism: A review using a computational context. *Journal of Autism and Developmental Disorders.* https://doi.org/10.1007/s10803-012-1574-0.

Green, D., Baird, G., Barnett, A. L., Henderson, L., Huber, J., & Henderson, S. E. (2002). The severity and nature of motor impairment in Asperger's syndrome: A comparison with specific developmental disorder of motor function. *Journal of Child Psychology and Psychiatry, 43*(5), 655−668. https://doi.org/10.1111/1469-7610.00054.

Green, D., Charman, T., Pickles, A., Chandler, S., Loucas, T., Simonoff, E., et al. (2009). Impairment in movement skills of children with autistic spectrum disorders. *Developmental Medicine and Child Neurology, 51*(4), 311−316. https://doi.org/10.1111/j.1469-8749.2008.03242.x.

Green, J. R., Moore, C. A., & Reilly, K. J. (2002). The sequential development of jaw and lip control for speech. *Journal of Speech, Language, and Hearing Research: JSLHR, 45*(1), 66−79. https://doi.org/10.1044/1092-4388(2002/005).

Grèzes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to "mirror" and "canonical" neurones in the human brain: An fMRI study. *NeuroImage, 18*(4), 928−937. https://doi.org/10.1016/S1053-8119(03)00042-9.

Grèzes, J., Frith, C. D., & Passingham, R. E. (2004). Inferring false beliefs from the actions of oneself and others: An fMRI study. *NeuroImage, 21*(2), 744−750. https://doi.org/10.1016/S1053-8119(03)00665-7.

Grisoni, L., Dreyer, F., & Pulvermüller, F. (2016). Somatotopic semantic priming and prediction in the motor system. *Cerebral Cortex*, 2353−2366. https://doi.org/10.1093/cercor/bhw026.

Grisoni, L., McCormick-Miller, T., & Pulvermüller, F. (2017). Neural correlates of semantic prediction and resolution in sentence processing. *Journal of Neuroscience.* https://doi.org/10.1523/JNEUROSCI.2800-16.2017, 2800−16.

Grossman, M., Anderson, C., Khan, A., Avants, B., Elman, L., & McCluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology, 71*(18), 1396−1401. https://doi.org/10.1212/01.wnl.0000319701.50168.8c.

Guinchat, V., Chamak, B., Bonniau, B., Bodeau, N., Perisse, D., Cohen, D., et al. (2012). Very early signs of autism reported by parents include many concerns not specific to autism criteria. *Research in Autism Spectrum Disorders, 6*(2), 589−601. https://doi.org/10.1016/j.rasd.2011.10.005.

Hamilton, A. F. D. C. (2013). Reflecting on the mirror neuron system in autism: A systematic review of current theories. *Developmental Cognitive Neuroscience.* https://doi.org/10.1016/j.dcn.2012.09.008.

Hamilton, A. (2016). The social function of the human mirror system: A motor chauvinist view. In S. S. Ohbi, & E. S. Cross (Eds.), *Shared representations: Sensorimotor foundations of social life* (pp. 313−332). Cambridge, UK: Cambridge University Press.

Hamilton, A. F., Brindley, R., & Frith, U. (2009). Visual perspective taking impairment in children with autistic spectrum disorder. *Cognition, 113*(1), 37−44. https://doi.org/10.1016/j.cognition.2009.07.007.

Hanaie, R., Mohri, I., Kagitani-Shimono, K., Tachibana, M., Azuma, J., Matsuzaki, J., et al. (2013). Altered microstructural connectivity of the superior cerebellar peduncle is related to motor dysfunction in children with autistic spectrum disorders. *The Cerebellum, 12*(5), 645−656. https://doi.org/10.1007/s12311-013-0475-x.

Hanaie, R., Mohri, I., Kagitani-Shimono, K., Tachibana, M., Matsuzaki, J., Hirata, I., et al. (2016). White matter volume in the brainstem and inferior parietal lobule is related to motor performance in children with autism spectrum disorder: A voxel-based morphometry study. *Autism Research, 9*(9), 981−992.

Hanaie, R., Mohri, I., Kagitani-Shimono, K., Tachibana, M., Matsuzaki, J., Watanabe, Y., et al. (2014). Abnormal corpus callosum connectivity, socio-communicative deficits, and motor deficits in children with autism spectrum disorder: A diffusion tensor imaging study. *Journal of Autism and Developmental Disorders, 44*(9), 2209−2220. https://doi.org/10.1007/s10803-014-2096-8.

Happé, F. G. (1994). An advanced test of theory of mind: Understanding of story characters' thoughts and feelings by able autistic, mentally handicapped, and normal children and adults. *Journal of Autism and Developmental Disorders, 24*, 129−154. https://doi.org/10.1007/BF02172093.

Happé, F. G. E. (1997). Central coherence and theory of mind in autism: Reading homographs in context. *British Journal of Developmental Psychology, 15*(1), 1−12. https://doi.org/10.1111/j.2044-835X.1997.tb00721.x.

Hardan, A. Y., Kilpatrick, M., Keshavan, M. S., & Minshew, N. J. (2003). Motor performance and anatomic magnetic resonance imaging (MRI) of the basal ganglia in autism. *Journal of Child Neurology, 18*(5), 317−324. https://doi.org/10.1177/08830738030180050801.

Harms, M. B., Martin, A., & Wallace, G. L. (2010). Facial emotion recognition in autism spectrum disorders: A review of behavioral and neuroimaging studies. *Neuropsychology Review.* https://doi.org/10.1007/s11065-010-9138-6.

Hauk, O. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience.* https://doi.org/10.3389/fnhum.2011.00149.

Hauck, J. A., & Dewey, D. (2001). Hand preference and motor functioning in children with autism. *Journal of Autism and*

Developmental Disorders, 31(3), 265–277. https://doi.org/10.1023/A:1010791118978.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*, 301–307. https://doi.org/10.1016/S0896-6273(03)00838-9.

Hauk, O., & Pulvermüller, F. (2011 November). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience, 5*, 1–10. https://doi.org/10.3389/fnhum.2011.00149.

Hauk, O., Shtyrov, Y., & Pulvermüller, F. (2008). The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology Paris, 102*, 50–58. https://doi.org/10.1016/j.jphysparis.2008.03.013.

Havas, D. A., Glenberg, A. M., Gutowski, K. A., Lucarelli, M. J., & Davidson, R. J. (2010). Cosmetic use of botulinum toxin-a affects processing of emotional language. *Psychological Science: A Journal of the American Psychological Society/APS, 21*, 895–900. https://doi.org/10.1177/0956797610374742.

Hazlett, H. C., Gu, H., Munsell, B. C., Kim, S. H., Styner, M., Wolff, J. J., et al. (2017). Early brain development in infants at high risk for autism spectrum disorder. *Nature, 542*(7641), 348–351.

Hebb, D. O. (1949). The organization of behaviour. *Organization.* http://doi.org/citeulike-article-id:1282862.

Heid, R., & Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *Journal of Comparative and Physiological Psychology, 56*, 872–876.

Hellendoorn, A., Wijnroks, L., van Daalen, E., Dietz, C., Buitelaar, J., & Leseman, P. (2015). Motor functioning, exploration, visuospatial cognition and language development in preschool children with autism. *Research in Developmental Disabilities, 39*, 32–42. https://doi.org/10.1016/j.ridd.2014.12.033.

Hendrickx, S. (2015). *Women and girls with autism spectrum disorder: Understanding life experiences from early childhood to old age.* London: Jessica Kingsley Publishers.

Herbet, G., Lafargue, G., Bonnetblanc, F., Moritz-Gasser, S., De Champfleur, N. M., & Duffau, H. (2014). Inferring a dual-stream model of mentalizing from associative white matter fibres disconnection. *Brain, 137*(3), 944–959.

Hermelin, B., & O'Connor, N. (1970). *Psychological experiments with autistic children.* Oxford, UK: Pergamon Press.

Hickok, G. (2010). The role of mirror neurons in speech and language processing. *Brain and Language, 112*(1), 1–2. https://doi.org/10.1016/j.bandl.2009.10.006.

Hickok, G. (2014). *The myth of mirror neurons: The real neuroscience of communication and cognition.* New York, NY: W. W. Norton and Company.

Hill, E. L. (2001). Non-specific nature of specific language impairment: A review of the literature with regard to concomitant motor impairments. *International Journal of Language & Communication Disorders, 36*(2), 149–171. https://doi.org/10.1080/13682820010019874.

Hilton, C., Wente, L., LaVesser, P., Ito, M., Reed, C., & Herzberg, G. (2007). Relationship between motor skill impairment and severity in children with Asperger syndrome. *Research in Autism Spectrum Disorders, 1*(4), 339–349. https://doi.org/10.1016/j.rasd.2006.12.003.

Hilton, C. L., Zhang, Y., Whilte, M. R., Klohr, C. L., & Constantino, J. (2012). Motor impairment in sibling pairs concordant and discordant for autism spectrum disorders. *Autism: The International Journal of Research and Practice, 16*(4), 430–441. https://doi.org/10.1177/1362361311423018.

Honaga, E., Ishii, R., Kurimoto, R., Canuet, L., Ikezawa, K., Takahashi, H., et al. (2010). Post-movement beta rebound abnormality as indicator of mirror neuron system dysfunction in autistic spectrum disorder: An MEG study. *Neuroscience*

Letters, 478(3), 141–145. https://doi.org/10.1016/j.neulet.2010.05.004.

Honey, C. J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J. P., Meuli, R., et al. (2009). Predicting human resting-state functional connectivity. *106*(6), 1–6.

Howlin, P. (2003). Outcome in high-functioning adults with autism with and without early language delays: Implications for the differentiation between autism and asperger syndrome. *Journal of Autism and Developmental Disorders, 33*(1), 3–13. https://doi.org/10.1023/A:1022270118899.

Hsu, H.-C., Chen, C.-L., Cheng, P.-T., Chen, C.-H., Chong, C.-Y., & Lin, Y.-Y. (2004). The relationship of social function with motor and speech functions in children with autism. *Chang Gung Medical Journal, 27*(10), 750–757. Retrieved from: http://www.ncbi.nlm.nih.gov/pubmed/15646298.

Hsu, H. C., & Iyer, S. N. (2016). Early gesture, early vocabulary, and risk of language impairment in preschoolers. *Research in Developmental Disabilities, 57*, 201–210.

Hubert, B., Wicker, B., Moore, D. G., Monfardini, E., Duverger, H., Da Fonséca, D., et al. (2007). Brief report: Recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *Journal of Autism and Developmental Disorders, 37*(7), 1386–1392. https://doi.org/10.1007/s10803-006-0275-y.

Hughes, C. (1996). Brief report: Planning problems in autism at the level of motor control. *Journal of Autism And Developmental Disorders, 26*(1), 99–107.

Humphreys, G. F., Hoffman, P., Visser, M., Binney, R. J., & Lambon Ralph, M. a (2015). Establishing task- and modality-dependent dissociations between the semantic and default mode networks. *Proceedings of the National Academy of Sciences, 112*(25). https://doi.org/10.1073/pnas.1422760112, 201422760.

Ibanez, A., Melloni, M., Huepe, D., Helgiu, E., Rivera-Rei, A., Canales-Johnson, A., et al. (2012). What event-related potentials (ERPs) bring to social neuroscience? *Social Neuroscience, 7*(6), 632–649. https://doi.org/10.1080/17470919.2012.691078.

Iverson, J. M. (2010). Developing language in a developing body: The relationship between motor development and language development. *Journal of Child Language, 37*(2), 229–261. https://doi.org/10.1017/S.

Iverson, J. M., & Goldin-Meadow, S. (2005). Gesture paves the way for language development. *Psychological Science, 16*(5), 367–371. https://doi.org/10.1111/j.0956-7976.2005.01542.x.

Iverson, J. M., Hall, A. J., Nickel, L., & Wozniak, R. H. (2007). The relationship between reduplicated babble onset and laterality biases in infant rhythmic arm movements. *Brain and Language, 101*(3), 198–207. https://doi.org/10.1016/j.bandl.2006.11.004.

Iverson, J. M., & Thelen, E. (1999). Hand, mouth and brain: The dynamic emergence of speech and gesture. *Journal of Consciousness Studies, 6*(11–12), 19–40. https://doi.org/10.1006/brcg.1998.1020.

Iverson, J. M., & Wozniak, R. H. (2007). Variation in vocal-motor development in infant siblings of children with autism. *Journal of Autism and Developmental Disorders, 37*(1), 158–170. https://doi.org/10.1007/s10803-006-0339-z.

Iwanaga, R., Kawasaki, C., & Tsuchida, R. (2000). Brief report: Comparison of sensory-motor and cognitive function between autism and Asperger syndrome in preschool children. *Journal of Autism and Developmental Disorders, 30*(2), 169–174. Retrieved from: http://www.ncbi.nlm.nih.gov/pubmed/10832782.

Izawa, J., Pekny, S. E., Marko, M. K., Haswell, C. C., Shadmehr, R., & Mostofsky, S. H. (2012). Motor learning relies on integrated sensory inputs in ADHD, but over-selectively on proprioception in autism spectrum conditions. *Autism Research, 5*(2), 124–136. https://doi.org/10.1002/aur.1222.

James, K. H., & Swain, S. N. (2011). Only self-generated actions create sensori-motor systems in the developing brain.

Developmental Science, 14(4), 673—678. https://doi.org/10.1111/j.1467-7687.2010.01011.x.

Jansiewicz, E. M., Goldberg, M. C., Newschaffer, C. J., Denckla, M. B., Landa, R., & Mostofsky, S. H. (2006). Motor signs distinguish children with high functioning autism and Asperger's syndrome from controls. *Journal of Autism and Developmental Disorders, 36*(5), 613—621. https://doi.org/10.1007/s10803-006-0109-y.

Järvinen-Pasley, A., Pasley, J., & Heaton, P. (2008). Is the linguistic content of speech less salient than its perceptual features in autism? *Journal of Autism and Developmental Disorders, 38*(2), 239—248.

Jasmin, E., Couture, M., McKinley, P., Reid, G., Fombonne, E., & Gisel, E. (2009). Sensori-motor and daily living skills of preschool children with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 39*(2), 231—241. https://doi.org/10.1007/s10803-008-0617-z.

Jolliffe, T., & Baron-Cohen, S. (1999). A test of central coherence theory: Linguistic processing in high-functioning adults with autism or Asperger syndrome: Is local coherence impaired? *Cognition, 71*(2), 149—185. https://doi.org/10.1016/S0010-0277(99)00022-0.

Kamio, Y., & Toichi, M. (2000). Dual access to semantics in autism: Is pictorial access superior to verbal access? *Journal of Child Psychology and Psychiatry, 41*(7), 859—867. https://doi.org/10.1111/1469-7610.00673.

Kana, R. K., Blum, E. R., Ladden, S. L., & Ver Hoef, L. W. (2012). "How to do things with Words": Role of motor cortex in semantic representation of action words. *Neuropsychologia, 50,* 3403—3409. https://doi.org/10.1016/j.neuropsychologia.2012.09.006.

Kanner, L. (1943). Autistic disturbances of affective contact. *Nervous Child, 2,* 217—250.

Karasik, L. B., Tamis-Lemonda, C. S., & Adolph, K. E. (2011). Transition from crawling to walking and infants' actions with objects and people. *Child Development, 82*(4), 1199—1209. https://doi.org/10.1111/j.1467-8624.2011.01595.x.

Karasik, L. B., Tamis-Lemonda, C. S., & Adolph, K. E. (2014). Crawling and walking infants elicit different verbal responses from mothers. *Developmental Science, 17*(3), 388—395. https://doi.org/10.1111/desc.12129.

van Kemenade, B. M., Muggleton, N., Walsh, V., & Saygin, A. P. (2012). Effects of TMS over premotor and superior temporal cortices on biological motion perception. *Journal of Cognitive Neuroscience, 24*(4), 896—904. https://doi.org/10.1162/jocn_a_00194.

Kemmerer, D. (2015). *Word order, action, and the brain: A reply to arbib.*

Kemmerer, D., Rudrauf, D., Manzel, K., & Tranel, D. (2012). Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex, 48,* 826—848. https://doi.org/10.1016/j.cortex.2010.11.001.

Kenny, L., Hattersley, C., Molins, B., Buckley, C., Povey, C., & Pellicano, E. (2016). Which terms should be used to describe autism? Perspectives from the UK autism community. *Autism, 20*(4), 442—462. https://doi.org/10.1177/1362361315588200.

Kern, J. K., Geier, D. A., King, P. G., Sykes, L. K., Mehta, J. A., & Geier, M. R. (2015). Shared brain connectivity issues, symptoms, and comorbidities in autism spectrum disorder, attention deficit/hyperactivity disorder, and tourette syndrome. *Brain Connectivity, 5*(6), 321—335. https://doi.org/10.1089/brain.2014.0324.

Keysers, C., & Gazzola, V. (2007). Integrating simulation and theory of mind: From self to social cognition. *Trends in Cognitive Sciences.* https://doi.org/10.1016/j.tics.2007.02.002.

Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., & Hoenig, K. (2008). The sound of concepts: Four markers for a link between auditory and conceptual brain systems. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 28,* 12224—12230. https://doi.org/10.1523/JNEUROSCI.3579-08.2008.

Kiefer, M., Sim, E.-J., Liebich, S., Hauk, O., & Tanaka, J. (2007). Experience-dependent plasticity of conceptual representations in human sensory-motor areas. *Journal of Cognitive Neuroscience, 19,* 525—542. https://doi.org/10.1162/jocn.2007.19.3.525.

Kiefer, M., Trumpp, N., Herrnberger, B., Sim, E. J., Hoenig, K., & Pulvermüller, F. (2012). Dissociating the representation of action- and sound-related concepts in middle temporal cortex. *Brain and Language, 122,* 120—125. https://doi.org/10.1016/j.bandl.2012.05.007.

Kilner, J. M., Neal, A., Weiskopf, N., Friston, K. J., & Frith, C. D. (2009). Evidence of mirror neurons in human inferior frontal gyrus. *Journal of Neuroscience, 29*(32), 10153—10159. https://doi.org/10.1523/JNEUROSCI.2668-09.2009.

Kite, D. M., Gullifer, J., & Tyson, G. A. (2013). Views on the diagnostic labels of autism and Asperger's disorder and the proposed changes in the DSM. *Journal of Autism and Developmental Disorders, 43*(7), 1682—1700.

Klin, A., Jones, W., Schultz, R., & Volkmar, F. (2003). The enactive mind, or from actions to cognition: Lessons from autism. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358*(1430), 345—360. https://doi.org/10.1098/rstb.2002.1202.

Klinger, L. G., & Dawson, G. (2001). Prototype formation in autism. *Development and Psychopathology, 13*(1), 111—124. https://doi.org/10.1017/S0954579401001080.

Klintwall, L., Holm, A., Eriksson, M., Carlsson, L. H., Olsson, M. B., Hedvall, Å., et al. (2011). Sensory abnormalities in autism. A brief report. *Research in Developmental Disabilities, 32*(2), 795—800. https://doi.org/10.1016/j.ridd.2010.10.021.

Koldewyn, K., Whitney, D., & Rivera, S. M. (2011). Neural correlates of coherent and biological motion perception in autism. *Developmental Science, 14*(5), 1075—1088. https://doi.org/10.1111/j.1467-7687.2011.01058.x.

Konrad, K., & Eickhoff, S. B. (2010). Is the ADHD brain wired differently? A review on structural and functional connectivity in attention deficit hyperactivity disorder. *Human Brain Mapping.* https://doi.org/10.1002/hbm.21058.

Kopp, S., Beckung, E., & Gillberg, C. (2010). Developmental coordination disorder and other motor control problems in girls with autism spectrum disorder and/or attention-deficit/hyperactivity disorder. *Research in Developmental Disabilities, 31*(2), 350—361. https://doi.org/10.1016/j.ridd.2009.09.017.

Kushki, A., Chau, T., & Anagnostou, E. (2011). Handwriting difficulties in children with autism spectrum disorders: A scoping review. *Journal of Autism and Developmental Disorders, 41*(12), 1706—1716. https://doi.org/10.1007/s10803-011-1206-0.

Lai, M.-C., Lombardo, M. V., Auyeung, B., Chakrabarti, B., & Baron-Cohen, S. (2015). Sex/gender differences and autism: Setting the scene for future research. *Journal of the American Academy of Child & Adolescent Psychiatry, 54*(1), 11—24. https://doi.org/10.1016/j.jaac.2014.10.003.

Lakoff, G. (1987). *Women, fire and dangerous things: What categories reveal about the mind.* Chicago: University of Chicago Press.

Lakoff, G., & Johnson, M. (1980). Conceptual metaphor in everyday language. *The Journal of Philosophy, 77,* 453—486. https://doi.org/10.2307/2025464.

Lalanne, C., Falissard, B., Golse, B., & Vaivre-Douret, L. (2012). Refining developmental coordination disorder subtyping with multivariate statistical methods. *BMC Medical Research Methodology, 12,* 107. https://doi.org/10.1186/1471-2288-12-107.

Lambon Ralph, M. A., Ehsan, S., Baker, G. A., & Rogers, T. T. (2012). Semantic memory is impaired in patients with unilateral anterior temporal lobe resection for temporal lobe epilepsy. *Brain, 135*(1), 242—258. https://doi.org/10.1093/brain/awr325.

Landa, R., & Garrett-Mayer, E. (2006). Development in infants with autism spectrum disorders: A prospective study. *Journal of Child Psychology and Psychiatry and Allied Disciplines, 47*(6), 629–638. https://doi.org/10.1111/j.1469-7610.2006.01531.x.

Landa, R. J., Gross, A. L., Stuart, E. A., & Bauman, M. (2012). Latent class analysis of early developmental trajectory in baby siblings of children with autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines, 53*(9), 986–996. https://doi.org/10.1111/j.1469-7610.2012.02558.x.

Landa, R. J., Gross, A. L., Stuart, E. A., & Faherty, A. (2013). Developmental trajectories in children with and without autism spectrum Disorders: The first 3 years. *Child Development, 84*(2), 429–442. https://doi.org/10.1111/j.1467-8624.2012.01870.x.

Langacker, R. W. (1987). *Theoretical prerequisites, foundations of cognitive grammar.* Stanford, CA: Oxford University Press.

Langdell, T. (1981). *Face perception: An approach to the study of autism.* University of London.

Langen, M., Schnack, H. G., Nederveen, H., Bos, D., Lahuis, B. E., de Jonge, M. V., et al. (2009). Changes in the developmental trajectories of striatum in autism. *Biological Psychiatry, 66*(4), 327–333. https://doi.org/10.1016/j.biopsych.2009.03.017.

Le Couteur, A., Lord, C., & Rutter, M. (2003). *The autism diagnostic interview-revised (ADI-R).* Los Angeles, CA: Western Psychological Services.

Leary, M. R., & Hill, D. A. (1996). Moving on: Autism and movement disturbance. *34*(1), 39–53.

Lebarton, E. S., & Iverson, J. M. (2013). Fine motor skill predicts expressive language in infant siblings of children with autism. *Developmental Science, 16*(6), 815–827. https://doi.org/10.1111/desc.12069.

Lee, K., Lambert, H., Wittich, W., & Park, M. (2016). The use of movement-based interventions with children diagnosed with autism for psychosocial outcomes—a scoping review. *Research in Autism Spectrum Disorders, 24*, 52–67.

Lenneberg, E. H. (1967). *Biological foundations of language.* New York, NY: Wiley and Sons.

Leonard, H. C., Bedford, R., Charman, T., Elsabbagh, M., Johnson, M. H., & Hill, E. L. (2014). Motor development in children at risk of autism: A follow-up study of infant siblings. *Autism: The International Journal of Research and Practice, 18*(3), 281–291. https://doi.org/10.1177/1362361312470037.

Leonard, H. C., Bedford, R., Pickles, A., & Hill, E. L. (2015). Predicting the rate of language development from early motor skills in at-risk infants who develop autism spectrum disorder. *Research in Autism Spectrum Disorders, 13–14*, 15–24. https://doi.org/10.1016/j.rasd.2014.12.012.

Leonard, H. C., & Hill, E. L. (2014). Review: The impact of motor development on typical and atypical social cognition and language: A systematic review. *Child & Adolescent Mental Health, 19*(3), 163–170.

Levit-Binnun, N., Davidovitch, M., & Golland, Y. (2013). Sensory and motor secondary symptoms as indicators of brain vulnerability. *Journal of Neurodevelopmental Disorders, 5*(1), 26. https://doi.org/10.1186/1866-1955-5-26.

Libertus, K., & Needham, A. (2011). Reaching experience increases face preference in 3-month-old infants. *Developmental Science, 14*(6), 1355–1364. https://doi.org/10.1111/j.1467-7687.2011.01084.x.

Linkenauger, S. A., Lerner, M. D., Ramenzoni, V. C., & Proffitt, D. R. (2012). A perceptual-motor deficit predicts social and communicative impairments in individuals with autism spectrum disorders. *Autism Research, 5*(5), 352–362. https://doi.org/10.1002/aur.1248.

Liszkowski, U. (2008). Before L1: A differentiated perspective on infant gestures. *Gesture, 8*(2), 180–196. https://doi.org/10.1075/gest.8.2.04lis.

Liuzzi, G., Freundlieb, N., Ridder, V., Hoppe, J., Heise, K., Zimerman, M., et al. (2010). The involvement of the left motor cortex in learning of a novel action word lexicon. *Current Biology, 20*, 1745–1751. https://doi.org/10.1016/j.cub.2010.08.034.

Lloyd, M., MacDonald, M., & Lord, C. (2013). Motor skills of toddlers with autism spectrum disorders. *Autism, 17*(2), 133–146. https://doi.org/10.1177/1362361311402230.

Locke, J. (1993). *The child's path to spoken language.* Cambridge, MA: Harvard University Press.

Locke, J. L., Bekken, K. E., Mcminnlarson, L., & Wein, D. (1995). Emergent control of manual and vocal-motor activity in relation to the development of speech. *Brain and Language, 51*(3), 498–508. https://doi.org/10.1006/brln.1995.1073.

Lombardo, M. V., & Baron-Cohen, S. (2011). The role of the self in mindblindness in autism. *Consciousness and Cognition, 20*, 130–140. https://doi.org/10.1016/j.concog.2010.09.006.

Lombardo, M. V., Chakrabarti, B., Bullmore, E. T., & Baron-Cohen, S. (2011). Specialization of right temporo-parietal junction for mentalizing and its relation to social impairments in autism. *NeuroImage, 56*, 1832–1838. https://doi.org/10.1016/j.neuroimage.2011.02.067.

Lombardo, M. V., Chakrabarti, B., Bullmore, E. T., Sadek, S. A., Pasco, G., Wheelwright, S. J., et al. (2010). Atypical neural self-representation in autism. *Brain: A Journal of Neurology, 133*, 611–624. https://doi.org/10.1093/brain/awp306.

Lombardo, M. V., Chakrabarti, B., Bullmore, E. T., Wheelwright, S. J., Sadek, S. A., Suckling, J., et al. (2010). Shared neural circuits for mentalizing about the self and others. *Journal of Cognitive Neuroscience, 22*, 1623–1635. https://doi.org/10.1162/jocn.2009.21287.

López, B., & Leekam, S. R. (2003). Do children with autism fail to process information in context? *Journal of Child Psychology and Psychiatry and Allied Disciplines, 44*(2), 285–300. https://doi.org/10.1111/1469-7610.00121.

Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Leventhal, B. L., Dilavore, P. C., et al. (2000). The autism diagnostic observation schedule-generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders, 30*, 205–223. https://doi.org/10.1023/A:1005592401947.

Lord, C., Risi, S., & Pickles, A. (2004). Trajectory of language development in autistic spectrum disorders. In M. Rice, & S. Warren (Eds.), *Developmental language disorders: From phenotypes to etiologies* (pp. 7–29). Mahwah, NJ: Lawrence Erlbaum Associates.

Lord, C., & Spence, S. J. (2006). Autism Spectrum Disorders: Phenotype and Diagnosis. In *Understanding autism: From basic neuroscience to treatment* (pp. 1–23). https://doi.org/10.1056/NEJMbkrev57295.

Loveland, K. A., Tunali-Kotoski, B., Pearson, D. A., Brelsford, K. A., et al. (1994). Imitation and expression of facial affect in autism. *Development & Psychopathology, 6*(3), 433–444. https://doi.org/10.1017/S0954579400006039.

Luyster, R. J., Kadlec, M. B., Carter, A., & Tager-Flusberg, H. (2008). Language assessment and development in toddlers with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 38*(8), 1426–1438. https://doi.org/10.1007/s10803-007-0510-1.

Macdonald, M., Lord, C., & Ulrich, D. (2013). The relationship of motor skills and adaptive behavior skills in young children with autism spectrum disorders. *Research in Autism Spectrum Disorders, 7*(11), 1383–1390. https://doi.org/10.1016/j.rasd.2013.07.020.

MacDonald, M., Lord, C., & Ulrich, D. A. (2013). The relationship of motor skills and social communicative skills in school-aged children with autism spectrum disorder. *Adapted Physical Activity Quarterly, 30*(3), 271–282. https://doi.org/10.1016/j.rasd.2013.07.020.

MacDonald, M., Lord, C., & Ulrich, D. A. (2014). Motor skills and calibrated autism severity in young children with autism spectrum disorder. *Adapted Physical Activity Quarterly: APAQ, 31*, 95–105. https://doi.org/10.1123/apaq.2013-0068.

Machery, E. (2007). Concept empiricism: A methodological critique. *Cognition, 104*, 19–46. https://doi.org/10.1016/j.cognition.2006.05.002.

Maestro, S., Muratori, F., Barbieri, F., Casella, C., Cattaneo, V., Cavallaro, M. C., et al. (2001). Early behavioral development in autistic children: the first 2 years of life through home movies. *Psychopathology, 34*(3), 147–152. https://doi.org/10.1159/000049298.

Maestro, S., Muratori, F., Cavallaro, M. C., Pei, F., Stern, D., Golse, B., et al. (2001). Attentional skills during the first 6 months of age in autism spectrum disorder. *American Academy of Child and Adolescent Psychiatry, 41*, 1239–1245. https://doi.org/10.1097/00004583-200210000-00014.

Maestro, S., Muratori, F., Cavallaro, M. C., Pei, F., Stern, D., Golse, B., et al. (2002). Attentional skills during the first 6 months of age in autism spectrum disorder. *Journal of the American Academy of Child & Adolescent Psychiatry, 41*(10), 1239–1245.

Mahajan, R., Dirlikov, B., Crocetti, D., & Mostofsky, S. H. (2015). Motor circuit anatomy in children with autism spectrum disorder with or without attention deficit hyperactivity disorder. *Autism Research*, 67–81. https://doi.org/10.1002/aur.1497.

Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology Paris, 102*, 59–70. https://doi.org/10.1016/j.jphysparis.2008.03.004.

Mahon, B., & Hickok, G. (2016). Arguments about the nature of concepts: Symbols, embodiment, and beyond. *Psychonomic Bulletin & Review*, 1–18.

Mandy, W. P. L., Charman, T., & Skuse, D. H. (2012). Testing the construct validity of proposed criteria for DSM-5 autism spectrum disorder. *Journal of the American Academy of Child and Adolescent Psychiatry, 51*(1), 41–50. https://doi.org/10.1016/j.jaac.2011.10.013.

Manjiviona, J., & Prior, M. (1995). Comparison of Asperger Syndrome and high-functioning autistic-children on a test of motor impairment. *Journal of Autism and Developmental Disorders, 25*(1), 23–39. https://doi.org/10.1007/bf02178165.

Marco, E. J., Hinkley, L. B. N., Hill, S. S., & Nagarajan, S. S. (2011). Sensory processing in autism: A review of neurophysiologic findings. *Pediatric Research, 69*(5 PART 2). https://doi.org/10.1203/PDR.0b013e3182130c54.

Mari, M., Castiello, U., Marks, D., Marraffa, C., & Prior, M. (2003). The reach-to-grasp movement in children with autism spectrum disorder. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358*(1430), 393–403. https://doi.org/10.1098/rstb.2002.1205.

Marko, M. K., Crocetti, D., Hulst, T., Donchin, O., Shadmehr, R., & Mostofsky, S. H. (2015). Behavioural and neural basis of anomalous motor learning in children with autism. *Brain: A Journal of Neurology, 138*(Pt 3), 784–797. https://doi.org/10.1093/brain/awu394.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology, 58*, 25–45. https://doi.org/10.1146/annurev.psych.57.102904.190143.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science (New York, N.Y.), 270*, 102–105. https://doi.org/10.1126/science.270.5233.102.

Marton, K. (2009). Imitation of body postures and hand movements in children with specific language impairment. *Journal of Experimental Child Psychology, 102*(1), 1–13. https://doi.org/10.1016/j.jecp.2008.07.007.

Matson, M. L., Matson, J. L., & Beighley, J. S. (2011). Comorbidity of physical and motor problems in children with autism. *Research in Developmental Disabilities, 32*(6), 2304–2308. https://doi.org/10.1016/j.ridd.2011.07.036.

Maurer, R. G., & Damasio, A. R. (1982). Childhood autism from the point of view of behavioral neurology. *Journal of Autism and Developmental Disorders, 12*(2), 195–205. https://doi.org/10.1007/BF01531309.

Mayes, A. K., Reilly, S., & Morgan, A. T. (2015). Neural correlates of childhood language disorder: A systematic review. *Developmental Medicine and Child Neurology*. https://doi.org/10.1111/dmcn.12714.

McAuliffe, D., Pillai, A. S., Tiedemann, A., Mostofsky, S. H., & Ewen, J. B. (2017). Dyspraxia in ASD: Impaired coordination of movement elements. *Autism Research, 10*(4), 648–652. https://doi.org/10.1002/aur.1693.

McCleery, J. P., Elliott, N. A., Sampanis, D. S., & Stefanidou, C. A. (2013). motor development and motor resonance difficulties in autism: relevance to early intervention for language and communication skills. *Frontiers in Integrative Neuroscience, 7*.

Mcdonald, H., Rutter, M., Howlin, P., Rios, P., Conteur, A., Evered, C., et al. (1989). Recognition and expression of emotional cues by autistic and normal adults. *Journal of Child Psychology and Psychiatry, 30*(6), 865–877.

McIntosh, D. N., Reichmann-Decker, A., Winkielman, P., & Wilbarger, J. L. (2006). When the social mirror breaks: Deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Developmental Science, 9*(3), 295–302. https://doi.org/10.1111/j.1467-7687.2006.00492.x.

McPhillips, M., Finlay, J., Bejerot, S., & Hanley, M. (2014). Motor deficits in children with autism spectrum disorder: a cross-syndrome study. *Autism Research, 7*(6), 664–676. https://doi.org/10.1002/aur.1408.

Meltzoff, A. N., & Decety, J. (2003). What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 358*(1431), 491–500. https://doi.org/10.1098/rstb.2002.1261.

Miller, M., Chukoskie, L., Zinni, M., Townsend, J., & Trauner, D. (2014). Dyspraxia, motor function and visual-motor integration in autism. *Behavioural Brain Research, 269*, 95–102. https://doi.org/10.1016/j.bbr.2014.04.011.

Minshew, N. J., & Goldstein, G. (1998). Autism as a disorder of complex information processing. *Mental Retardation and Developmental Disabilities Research Reviews*. https://doi.org/10.1002/(SICI)1098-2779(1998)4:2<129::AID-MRDD10>3.0.CO;2-X.

Miyahara, M. (2013). Meta review of systematic and meta analytic reviews on movement differences, effect of movement based interventions, and the underlying neural mechanisms in autism spectrum disorder. *Frontiers in Integrative Neuroscience, 7*, 16. https://doi.org/10.3389/fnint.2013.00016.

Miyahara, M., Tsujii, M., Hori, M., Nakanishi, K., Kageyama, H., & Sugiyama, T. (1997). Brief report: motor incoordination in children with Asperger syndrome and learning disabilities. *Journal of Autism and Developmental Disorders, 27*(5), 595–603. https://doi.org/10.1023/a:1025834211548.

Mody, M., Shui, A. M., Nowinski, L. A., Golas, S. B., Ferrone, C., O'Rourke, J. A., et al. (2017). Communication deficits and the motor system: exploring patterns of associations in autism spectrum disorder (ASD). *Journal of Autism and Developmental Disorders, 47*(1), 155–162. https://doi.org/10.1007/s10803-016-2934-y.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2011.07.004.

Molloy, C. A., Dietrich, K. N., & Bhattacharya, A. (2003). postural stability in children with autism spectrum disorder. *Journal of Autism and Developmental Disorders, 33*(6), 643–652. https://doi.org/10.1023/B:JADD.0000006001.00667.4c.

Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More than mere mimicry? The influence of emotion on rapid facial reactions to faces. *Emotion (Washington, D.C.), 7*(2), 447–457. https://doi.org/10.1037/1528-3542.7.2.447.

Moscoso Del Prado Martín, F., Hauk, O., & Pulvermüller, F. (2006). Category specificity in the processing of color-related and form-related words: An ERP study. *NeuroImage, 29*, 29–37. https://doi.org/10.1016/j.neuroimage.2005.07.055.

Moseley, R., Carota, F., Hauk, O., Mohr, B., & Pulvermüller, F. (2012). A role for the motor system in binding abstract emotional meaning. *Cerebral Cortex, 22*, 1634–1647. https://doi.org/10.1093/cercor/bhr238.

Moseley, R., Correia, M., Baron-Cohen, S., Shtyrov, Y., Pulvermüller, F., & Mohr, B. (2016). Reduced volume of the arcuate fasciculus in adults with high-functioning autism spectrum conditions. *Frontiers in Human Neuroscience, 10*.

Moseley, R. L., Mohr, B., Lombardo, M. V., Baron-Cohen, S., Hauk, O., & Pulvermüller, F. (2013). Brain and behavioral correlates of action semantic deficits in autism. *Frontiers in Human Neuroscience, 7*, 725. https://doi.org/10.3389/fnhum.2013.00725.

Moseley, R. L., Pulvermüller, F., Mohr, B., Lombardo, M. V., Baron-Cohen, S., & Shtyrov, Y. (2014). Brain routes for reading in adults with and without autism: EMEG evidence. *Journal of Autism and Developmental Disorders, 44*, 137–153. https://doi.org/10.1007/s10803-013-1858-z.

Moseley, R. L., Pulvermüller, F., & Shtyrov, Y. (2013). Sensorimotor semantics on the spot: brain activity dissociates between conceptual categories within 150 ms. *Scientific Reports, 3*, 1928. https://doi.org/10.1038/srep01928.

Moseley, R. L., Shtyrov, Y., Mohr, B., Lombardo, M. V., Baron-Cohen, S., & Pulvermüller, F. (2015). Lost for emotion words: What motor and limbic brain activity reveals about autism and semantic theory. *NeuroImage, 104*, 413–422. https://doi.org/10.1016/j.neuroimage.2014.09.046.

Moseley, R. L., Ypma, R. J. F., Holt, R. J., Floris, D., Chura, L. R., Spencer, M. D., et al. (2015). Whole-brain functional hypoconnectivity as an endophenotype of autism in adolescents. *NeuroImage: Clinical, 9*, 140–152.

Mostofsky, S. H., Burgess, M. P., & Gidley Larson, J. C. (2007). Increased motor cortex white matter volume predicts motor impairment in autism. *Brain, 130*, 2117–2122. https://doi.org/10.1093/brain/awm129.

Mostofsky, S. H., & Ewen, J. B. (2011). Altered connectivity and action model formation in autism is autism. *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry, 17*, 437–448. https://doi.org/10.1177/1073858410392381.

Mostofsky, S. H., Powell, S. K., Simmonds, D. J., Goldberg, M. C., Caffo, B., & Pekar, J. J. (2009). Decreased connectivity and cerebellar activity in autism during motor task performance. *Brain, 132*(9), 2413–2425. https://doi.org/10.1093/brain/awp088.

Möttönen, R., Dutton, R., & Watkins, K. E. (2013). Auditory-motor processing of speech sounds. *Cerebral Cortex (New York, N.Y.: 1991), 23*(5), 1190–1197. https://doi.org/10.1093/cercor/bhs110.

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology, 20*(8), 750–756. https://doi.org/10.1016/j.cub.2010.02.045.

Mulligan, S., & White, B. P. (2012). Sensory and motor behaviors of infant siblings of children with and without autism. *American Journal of Occupational Therapy, 66*(5), 556–566. https://doi.org/10.5014/ajot.2012.004077.

Murakami, T., Kell, C., Restle, J., Ugawa, Y., & Ziemann, U. (2015). Left dorsal speech stream components and their contribution to phonological processing. *Journal of Neuroscience, 35*(4), 1411–1422.

Nayate, A., Bradshaw, J. L., & Rinehart, N. J. (2005). Autism and Asperger's disorder: are they movement disorders involving the cerebellum and/or basal ganglia? *Brain Research Bulletin, 67*(4), 327–334. https://doi.org/10.1016/j.brainresbull.2005.07.011.

Nazarali, N., Glazebrook, C. M., & Elliott, D. (2009). Movement planning and reprogramming in individuals with autism. *Journal of Autism and Developmental Disorders, 39*(10), 1401–1411. https://doi.org/10.1007/s10803-009-0756-x.

Neal, D. T., & Chartrand, T. L. (2011). Embodied emotion perception: amplifying and dampening facial feedback modulates emotion perception accuracy. *Social Psychological and Personality Science*. https://doi.org/10.1177/1948550611406138.

Nebel, M. B., Eloyan, A., Barber, A. D., & Mostofsky, S. H. (2014). Precentral gyrus functional connectivity signatures of autism. *Frontiers in Systems Neuroscience, 8*, 80. https://doi.org/10.3389/fnsys.2014.00080.

Nebel, M. B., Eloyan, A., Nettles, C. A., Sweeney, K. L., Ament, K., Ward, R. E., et al. (2016). Intrinsic visual-motor synchrony correlates with social deficits in autism. *Biological Psychiatry, 79*(8), 633–641. https://doi.org/10.1016/j.biopsych.2015.08.029.

Nebel, M. B., Joel, S. E., Muschelli, J., Barber, A. D., Caffo, B. S., Pekar, J. J., et al. (2014). Disruption of functional organization within the primary motor cortex in children with autism. *Human Brain Mapping, 35*(2), 567–580. https://doi.org/10.1002/hbm.22188.

Needham, A., & Libertus, K. (2011). Embodiment in early development. *Wiley Interdisciplinary Reviews: Cognitive Science, 2*(1), 117–123. https://doi.org/10.1002/wcs.109.

Neininger, B., & Pulvermüller, F. (2001). The right hemisphere's role in action word processing: a double case study. *Neurocase: Case Studies in Neuropsychology, Neuropsychiatry, and Behavioural Neurology, 7*(4), 303–317. https://doi.org/10.1093/neucas/7.4.303.

Neininger, B., & Pulvermüller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia, 41*(1), 53–70. https://doi.org/10.1016/S0028-3932(02)00126-4.

Newschaffer, C. J., Croen, L. A., Fallin, M. D., Hertz-Picciotto, I., Nguyen, D. V., Lee, N. L., et al. (2012). Infant siblings and the investigation of autism risk factors. *Journal of Neurodevelopmental Disorders, 4*(1), 7. https://doi.org/10.1186/1866-1955-4-7.

Nickel, L. R., Thatcher, A. R., Keller, F., Wozniak, R. H., & Iverson, J. M. (2013). Posture development in infants at heightened versus low risk for autism spectrum disorders. *Infancy, 18*(5), 639–661. https://doi.org/10.1111/infa.12025.

Nip, I. S. B., Green, J. R., & Marx, D. B. (2009). Early speech motor development: Cognitive and linguistic considerations. *Journal of Communication Disorders, 42*(4), 286–298. https://doi.org/10.1016/j.jcomdis.2009.03.008.

Nishitani, N., Avikainen, S., & Hari, R. (2004). Abnormal imitation-related cortical activation sequences in Asperger's syndrome. *Annals of Neurology, 55*(4), 558–562. https://doi.org/10.1002/ana.20031.

Nobile, M., Perego, P., Piccinini, L., Mani, E., Rossi, A., Bellina, M., et al. (2011). Further evidence of complex motor dysfunction in drug naive children with autism using automatic motion analysis of gait. *Autism, 15*(3), 263–283. https://doi.org/10.1177/1362361309356929.

Nomi, J. S., & Uddin, L. Q. (2015). Developmental changes in large-scale network connectivity in autism. *NeuroImage: Clinical, 7*, 732–741. https://doi.org/10.1016/j.nicl.2015.02.024.

Noterdaeme, M., Mildenberger, M., Minow, F., & Amorosa, A. (2002). Evaluation of neuromotor deficits in children with autism and children with a specific speech and language disorder. *Psychiatry, European Journal of Child and Adolescent, 11*, 219–225.

Oberman, L. M., Hubbard, E. M., McCleery, J. P., Altschuler, E. L., Ramachandran, V. S., & Pineda, J. A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Cognitive Brain Research, 24*, 190–198. https://doi.org/10.1016/j.cogbrainres.2005.01.014.

Oberman, L. M., Ramachandran, V. S., & Pineda, J. a (2008). Modulation of mu suppression in children with autism spectrum disorders in response to familiar or unfamiliar stimuli: the mirror neuron hypothesis. *Neuropsychologia, 46*(5), 1558–1565. https://doi.org/10.1016/j.neuropsychologia.2008.01.010.

Oberman, L. M., Winkielman, P., & Ramachandran, V. S. (2007). Face to face: blocking facial mimicry can selectively impair recognition of emotional expressions. *Social Neuroscience, 2*(3–4), 167–178. https://doi.org/10.1080/17470910701391943.

Osterling, J. A., Dawson, G., & Munson, J. A. (2002). Early recognition of 1-year-old infants with autism spectrum disorder versus mental retardation. *Development and Psychopathology, 14*(2), 239–251. https://doi.org/10.1017/S0954579402002031.

Ozonoff, S., Iosif, A.-M., Baguio, F., Cook, I. C., Hill, M. M., Hutman, T., et al. (2010). A Prospective study of the emergence of early behavioral signs of autism. *Journal of the American Academy of Child & Adolescent Psychiatry, 49*(3), 256–266.e2. https://doi.org/10.1016/j.jaac.2009.11.009.

Ozonoff, S., Young, G. S., Belding, A., Hill, M., Hill, A., Hutman, T., et al. (2014). The broader autism phenotype in infancy: When does it emerge? *Journal of the American Academy of Child and Adolescent Psychiatry, 53*(4). https://doi.org/10.1016/j.jaac.2013.12.020.

Ozonoff, S., Young, G. S., Goldring, S., Greiss-Hess, L., Herrera, A. M., Steele, J., et al. (2008). Gross motor development, movement abnormalities, and early identification of autism. *Journal of Autism and Developmental Disorders, 38*(4), 644–656. https://doi.org/10.1007/s10803-007-0430-0.

Ozonoff, S., Young, G. S., Steinfeld, M. B., Hill, M. M., Cook, I., Hutman, T., et al. (2009). How early do parent concerns predict later autism diagnosis? *Journal of Developmental and Behavioral Pediatrics: JDBP, 30*(5), 367–375. https://doi.org/10.1097/DBP.0b013e3181ba0fcf.

Özçalışkan, Ş., Adamson, L. B., & Dimitrova, N. (2015). Early deictic but not other gestures predict later vocabulary in both typical development and autism. *Autism: The International Journal of Research and Practice*, 1–10. https://doi.org/10.1177/1362361315605921.

Palm, G., Knoblauch, A., Hauser, F., & Schüz, A. (2014). Cell assemblies in the cerebral cortex. *Biological Cybernetics*. https://doi.org/10.1007/s00422-014-0596-4.

Palomo, R., Belinchón, M., & Ozonoff, S. (2006). Autism and family home movies: a comprehensive review. *Journal of Developmental & Behavioral Pediatrics, 27*(Suppl. 2), S59–S68. https://doi.org/10.1097/00004703-200604002-00003.

Pan, C.-Y. (2014). Motor proficiency and physical fitness in adolescent males with and without autism spectrum disorders. *Autism, 18*(2), 156–165. https://doi.org/10.1177/1362361312458597.

Pan, C. Y., Tsai, C. L., & Chu, C. H. (2009). Fundamental movement skills in children diagnosed with autism spectrum disorders and attention deficit hyperactivity disorder. *Journal of Autism and Developmental Disorders, 39*(12), 1694–1705. https://doi.org/10.1007/s10803-009-0813-5.

Papadopoulos, N., McGinley, J., Tonge, B., Bradshaw, J., Saunders, K., Murphy, A., et al. (2012). Motor proficiency and emotional/behavioural disturbance in autism and Asperger's disorder: another piece of the neurological puzzle? *Autism: The International Journal of Research and Practice, 16*(6), 627–640. https://doi.org/10.1177/1362361311418692.

Paquet, A., Olliac, B., Bouvard, M. P., Golse, B., & Vaivre-Douret, L. (2016). The semiology of motor disorders in autism spectrum disorders as highlighted from a standardized neuro-psychomotor assessment. *Frontiers in Psychology, 7*. https://doi.org/10.3389/fpsyg.2016.01292.

Parma, V., & de Marchena, A. B. (2015). Motor signatures in Autism Spectrum Disorder: The importance of variability. *Journal of Neurophysiology*, 1522–1598. https://doi.org/10.1152/jn.00647.2015 (Electronic).

Patel, D., Fleming, S. M., & Kilner, J. M. (2012). Inferring subjective states through the observation of actions. *Proceedings of the Royal Society B: Biological Sciences, 279*(1748), 4853–4860. https://doi.org/10.1098/rspb.2012.1847.

Patten, E., Belardi, K., Baranek, G. T., Watson, L. R., Labban, J. D., & Oller, D. K. (2014). Vocal patterns in infants with autism spectrum disorder: Canonical babbling status and vocalization frequency. *Journal of Autism and Developmental Disorders, 44*(10), 2413–2428. https://doi.org/10.1007/s10803-014-2047-4.

Pearson, A., Ropar, D., & Hamilton, A. F. (2013). A review of visual perspective taking in autism spectrum disorder. *Frontiers in Human Neuroscience, 7*, 652. https://doi.org/10.3389/fnhum.2013.00652.

Perego, P., Forti, S., Crippa, A., Valli, A., & Reni, G. (2009). Reach and throw movement analysis with support vector machines in early diagnosis of autism. In *Conference proceedings … Annual international conference of the IEEE Engineering in Medicine and Biology Society* (pp. 2555–2558). IEEE Engineering in Medicine and Biology Society. https://doi.org/10.1109/IEMBS.2009.5335096.

Phagava, H., Muratori, F., Einspieler, C., Maestro, S., Apicella, F., Guzzetta, A., et al. (2008). General movements in infants with autism spectrum disorders. *Georgian Medical News, 156*, 100–105.

Piek, J. P., Bradbury, G. S., Elsley, S. C., & Tate, L. (2008). Motor Coordination and social–emotional behaviour in preschool-aged children. *International Journal of Disability, Development and Education, 55*(2), 143–151. https://doi.org/10.1080/10349120802033592.

Plumb, A. M., & Wetherby, A. M. (2013). Vocalization development in toddlers with autism spectrum disorder. *Journal of Speech, Language, and Hearing Research, 56*(2), 721–734. https://doi.org/10.1044/1092-4388(2012/11-0104).

Pobric, G., Jefferies, E., & Lambon Ralph, M. A. (2010). Amodal semantic representations depend on both anterior temporal lobes: Evidence from repetitive transcranial magnetic stimulation. *Neuropsychologia, 48*(5), 1336–1342. https://doi.org/10.1016/j.neuropsychologia.2009.12.036.

Pulvermüller, F. (1999). Words in the brain's language. *The Behavioral and Brain Sciences, 22*. https://doi.org/10.1017/S0140525X9900182X, 253–279–336.

Pulvermüller, F. (2012). Meaning and the brain: The neurosemantics of referential, interactive, and combinatorial knowledge. *Journal of Neurolinguistics, 25*, 423–459. https://doi.org/10.1016/j.jneuroling.2011.03.004.

Pulvermüller, F. (2013). How neurons make meaning: Brain mechanisms for embodied and abstract-symbolic semantics. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2013.06.004.

Pulvermüller, F., Cooper-Pye, E., Dine, C., Hauk, O., Nestor, P. J., & Patterson, K. (2010). The word processing deficit in semantic dementia: all categories are equal, but some categories are more equal than others. *Journal of Cognitive Neuroscience, 22*, 2027–2041. https://doi.org/10.1162/jocn.2009.21339.

Pulvermüller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nature Reviews. Neuroscience, 11*, 351–360. https://doi.org/10.1038/nrn2811.

Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *European Journal of Neuroscience, 21*, 793–797. https://doi.org/10.1111/j.1460-9568.2005.03900.x.

Pulvermüller, F., Moseley, R. L., Egorova, N., Shebani, Z., & Boulenger, V. (2014). Motor cognition-motor semantics: Action perception theory of cognition and communication. *Neuropsychologia, 55*(1), 71–84. https://doi.org/10.1016/j.neuropsychologia.2013.12.002.

Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience, 17*.

Puzzo, I., Cooper, N. R., Vetter, P., Russo, R., & Fitzgerald, P. B. (2009). Reduced cortico-motor facilitation in a normal sample with high traits of autism. *Neuroscience Letters, 467*(2), 173–177. https://doi.org/10.1016/j.neulet.2009.10.033.

Qiu, A., Adler, M., Crocetti, D., Miller, M. I., & Mostofsky, S. H. (2010). Basal ganglia shapes predict social, communication, and motor dysfunctions in boys with autism spectrum disorder. *Journal of the American Academy of Child and Adolescent Psychiatry, 49*(6). https://doi.org/10.1016/j.jaac.2010.02.012, 539–51, 551–554.

Ramachandran, V. S., & Oberman, L. M. (2006). Broken mirrors: A theory of autism. *Scientific American, 295*(5), 62–69.

Rice, G. E., Ralph, M. A. L., & Hoffman, P. (2015). The roles of left versus right anterior temporal lobes in conceptual knowledge: An ALE meta-analysis of 97 functional neuroimaging studies. *Cerebral Cortex, 25*(11), 4374–4391. https://doi.org/10.1093/cercor/bhv024.

Rinehart, N. J., Bellgrove, M. A., Tonge, B. J., Brereton, A. V., Howells-Rankin, D., & Bradshaw, J. L. (2006). An examination of movement kinematics in young people with high-functioning autism and Asperger's disorder: Further evidence for a motor planning deficit. *Journal of Autism and Developmental Disorders, 36*(6), 757–767. https://doi.org/10.1007/s10803-006-0118-x.

Rinehart, N. J., Bradshaw, J. L., Brereton, A. V., & Tonge, B. J. (2001). Movement preparation in high-functioning autism and asperger disorder: A serial choice reaction time task involving motor reprogramming. *Journal of Autism and Developmental Disorders, 31*(1), 79–88. https://doi.org/10.1023/A:1005617831035.

Rinehart, N., & McGinley, J. (2010). Is motor dysfunction core to autism spectrum disorder? *Developmental Medicine & Child Neurology, 52*(8), 697–697.

Rinehart, N. J., Tonge, B. J., Bradshaw, J. L., Iansek, R., Enticott, P. G., & McGinley, J. (2006). Gait function in high-functioning autism and Asperger's disorder: Evidence for basal-ganglia and cerebellar involvement? *European Child and Adolescent Psychiatry, 15*(5), 256–264. https://doi.org/10.1007/s00787-006-0530-y.

Rinehart, N. J., Tonge, B. J., Iansek, R., McGinley, J., Brereton, A. V., Enticott, P. G., et al. (2006). Gait function in newly diagnosed children with autism: Cerebellar and basal ganglia related motor disorder. *Developmental Medicine and Child Neurology, 48*(10), 819–824. https://doi.org/10.1017/S0012162206001769.

Rizzolatti, G., & Fabbri-Destro, M. (2010). Mirror neurons: From discovery to autism. *Experimental Brain Research*. https://doi.org/10.1007/s00221-009-2002-3.

Rizzolatti, G., Fabbri-Destro, M., & Cattaneo, L. (2009). Mirror neurons and their clinical relevance. *Neurology, 5*(1), 24–34. https://doi.org/10.1038/ncpneuro.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*(2), 131–141. https://doi.org/10.1016/0926-6410(95)00038-0.

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience, 11*(4), 264–274. https://doi.org/10.1038/nrn2805.

Roberts, T. P. L., Heiken, K., Zarnow, D., Dell, J., Nagae, L., Blaskey, L., et al. (2014). Left hemisphere diffusivity of the arcuate fasciculus: Influences of autism spectrum disorder and language impairment. *American Journal of Neuroradiology, 35*(3), 587–592. https://doi.org/10.3174/ajnr.A3754.

Robinson, E., St Pourcain, B., Anttila, V., Kosmicki, J., Bulik-Sullivan, B., Grove, J., et al. (2016). Genetic risk for autism spectrum disorders and neuropsychiatric variation in the general population. *Nature Genetics*. https://doi.org/10.1038/ng.3529.

Robledo, J., Donnellan, A. M., & Strandt-Conroy, K. (2012). An exploration of sensory and movement differences from the perspective of individuals with autism. *Frontiers in Integrative Neuroscience, 6*.

Rogers, T. D., McKimm, E., Dickson, P. E., Goldowitz, D., Blaha, C. D., & Mittleman, G. (2013). Is autism a disease of the cerebellum? An integration of clinical and pre-clinical research. *Frontiers in Systems Neuroscience, 7*, 15. https://doi.org/10.3389/fnsys.2013.00015.

Rothi, L. J. G., & Heilman, K. M. (Eds.). (1997). *Apraxia: the Neuropsychology of Action*. Hove: UK Psychology Press.

Rubenstein, J. L. R., & Merzenich, M. M.. (2003). Model of autism: increased ratio of excitation/inhibition in key neural systems, 255–267. http://doi.org/10.1046/j.1601-183X.2003.00037.x.

Rueschemeyer, S. A., Lindemann, O., van Elk, M., & Bekkering, H. (2009). Embodied cognition: The interplay between automatic resonance and selection-for-action mechanisms. *European Journal of Social Psychology, 39*, 1180–1187. https://doi.org/10.1002/ejsp.662.

Sachse, M., Schlitt, S., Hainz, D., Ciaramidaro, A., Schirman, S., Walter, H., et al. (2013). Executive and visuo-motor function in adolescents and adults with autism spectrum disorder. *Journal of Autism and Developmental Disorders, 43*(5), 1222–1235. https://doi.org/10.1007/s10803-012-1668-8.

Sacrey, L. A. R., Zwaigenbaum, L., Bryson, S., Brian, J., Smith, I. M., Roberts, W., et al. (2015). Can parents' concerns predict autism spectrum disorder? A prospective study of high-risk siblings from 6 to 36 months of age. *Journal of the American Academy of Child and Adolescent Psychiatry, 54*(6), 470–478. https://doi.org/10.1016/j.jaac.2015.03.014.

Saint-Georges, C., Cassel, R. S., Cohen, D., Chetouani, M., Laznik, M. C., Maestro, S., et al. (2010). What studies of family home movies can teach us about autistic infants: A literature review. *Research in Autism Spectrum Disorders*. https://doi.org/10.1016/j.rasd.2009.10.017.

Sartori, L., Becchio, C., Bara, B. G., & Castiello, U. (2009). Does the intention to communicate affect action kinematics? *Consciousness and Cognition, 18*(3), 766–772. https://doi.org/10.1016/j.concog.2009.06.004.

Scambler, D. J., Hepburn, S., Rutherford, M. D., Wehner, E. A., & Rogers, S. J. (2007). Emotional responsivity in children with autism, children with other developmental disabilities, and children with typical development. *Journal of Autism and Developmental Disorders, 37*(3), 553–563. https://doi.org/10.1007/s10803-006-0186-y.

Schippers, M. B., Roebroeck, A., Renken, R., Nanetti, L., & Keysers, C. (2010). Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 9388–9393. https://doi.org/10.1073/pnas.1001791107.

Schmitz, C., Martineau, J., Barthélémy, C., & Assaiante, C. (2003). Motor control and children with autism: Deficit of anticipatory function? *Neuroscience Letters, 348*(1), 17–20. https://doi.org/10.1016/S0304-3940(03)00644-X.

Schoen, E., Paul, R., & Chawarska, K. (2011). Phonology and vocal behavior in toddlers with autism spectrum disorders. *Autism Research, 4*(3), 177–188. https://doi.org/10.1002/aur.183.

Schomers, M. R., Garagnani, M., & Pulvermüller, F. (2017). Neurocomputational consequences of evolutionary connectivity changes in perisylvian language cortex. *Journal of Neuroscience, 37*(11), 3045–3055.

Schomers, M. R., Kirilina, E., Weigand, A., Bajbouj, M., & Pulvermüller, F. (2015). Causal influence of articulatory motor cortex on comprehending single spoken words: TMS evidence. *Cerebral Cortex, 25*(10), 3894–3902. https://doi.org/10.1093/cercor/bhu274.

Schomers, M. R., & Pulvermüller, F. (2016). Is the sensorimotor cortex relevant for speech perception and understanding? An integrative review. *Frontiers in Human Neuroscience, 10*, 435. https://doi.org/10.3389/fnhum.2016.00435.

Senju, A. (2013). Atypical development of spontaneous social cognition in autism spectrum disorders. *Brain & Development, 35*(2), 96–101. https://doi.org/10.1016/j.braindev.2012.08.002.

Sharer, E. A., Mostofsky, S. H., Pascual-Leone, A., & Oberman, L. M. (2015). Isolating visual and proprioceptive components of motor sequence learning in ASD. *Autism Research*. https://doi.org/10.1002/aur.1537.

Shebani, Z., & Pulvermüller, F. (2013). Moving the hands and feet specifically impairs working memory for arm- and leg-related action words. *Cortex, 49*, 222–231. https://doi.org/10.1016/j.cortex.2011.10.005.

Shtyrov, Y., Butorina, A., Nikolaeva, A., & Stroganova, T. (2014). Automatic ultrarapid activation and inhibition of cortical motor systems in spoken word comprehension. *Proceedings of the National Academy of Sciences of the United States of America, 111*(18), E1918–E1923. https://doi.org/10.1073/pnas.1323158111.

Shtyrov, Y., Hauk, O., & Pulvermüller, F. (2004). Distributed neuronal networks for encoding category-specific semantic information: The mismatch negativity to action words. *European Journal of Neuroscience, 19*, 1083–1092. https://doi.org/10.1111/j.0953-816X.2004.03126.x.

Simmons, W. K., & Barsalou, L. W. (2003). The similarity-in-topography principle: reconciling theories of conceptual deficits. *Cognitive Neuropsychology, 20*, 451–486. https://doi.org/10.1080/02643290342000032.

Simmons, W. K., Ramjee, V., Beauchamp, M. S., McRae, K., Martin, A., & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia, 45*, 2802–2810. https://doi.org/10.1016/j.neuropsychologia.2007.05.002.

Sinclair, J. (2013). Why I dislike "person first" language. *Autonomy, the Critical Journal of Interdisciplinary Autism Studies, 1*(2). original version 1999.

Sipes, M., Matson, J. L., & Horovitz, M. (2011). Autism spectrum disorders and motor skills: The effect on socialization as measured by the Baby and Infant Screen for Children with aUtIsm Traits (BISCUIT). *Developmental Neurorehabilitation, 14*(5), 290–296. https://doi.org/10.3109/17518423.2011.587838.

Skipper, J., Devlin, J., & Lametti, D. (2017). Is the hearing ear is always found close to the speaking tongue?: Review of the role of the motor system in speech perception. *Brain and Language, 164*, 77–105.

Smalle, E. H. M., Rogers, J., & Möttönen, R. (2015). Dissociating contributions of the motor cortex to speech perception and response bias by using transcranial magnetic stimulation. *Cerebral Cortex, 25*(10), 3690–3698. https://doi.org/10.1093/cercor/bhu218.

Smith, L. B., Suanda, S. H., & Yu, C. (2014). The unrealized promise of infant statistical word-referent learning. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2014.02.007.

Snowling, M., & Frith, U. (1986). Comprehension in "hyperlexic" readers. *Journal of Experimental Child Psychology, 42*(3), 392–415. https://doi.org/10.1016/0022-0965(86)90033-0.

Sperduti, M., Guionnet, S., Fossati, P., & Nadel, J. (2014). Mirror neuron system and mentalizing system connect during online social interaction. *Cognitive Processing, 15*(3), 307–316. https://doi.org/10.1007/s10339-014-0600-x.

Spreng, R. N., & Grady, C. L. (2010). Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *Journal of Cognitive Neuroscience, 22*, 1112–1123. https://doi.org/10.1162/jocn.2009.21282.

Spreng, R. N., Mar, R. A., & Kim, A. S. N. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *Journal of Cognitive Neuroscience, 21*(3), 489–510. https://doi.org/10.1162/jocn.2008.21029.

Spunt, R., & Lieberman, M. (2012). An integrative model of the neural systems supporting the comprehension of observed emotional behavior. *NeuroImage, 59*(3), 3050–3059. https://doi.org/10.1016/j.neuroimage.2011.10.005.

Staples, K. L., & Reid, G. (2010). Fundamental movement skills and autism spectrum disorders. *Journal of Autism and Developmental Disorders, 40*(2), 209–217. https://doi.org/10.1007/s10803-009-0854-9.

Stel, M., & van Knippenberg, A. (2008). The role of facial mimicry in the recognition of affect. *Psychological Science, 19*(10), 984–985.

Stern, D. N. (2000). *The interpersonal world of the infant*. New York, NY: Basic Books.

Stevenson, J. L., Lindley, C. E., & Murlo, N. (2017). Retrospectively assessed early motor and current pragmatic language skills in autistic and neurotypical children. *Perceptual and Motor Skills*. https://doi.org/10.1177/0031512517710379, 3151251771037.

Stoit, A. M. B., Van Schie, H. T., Slaats-Willemse, D. I. E., & Buitelaar, J. K. (2013). Grasping motor impairments in autism: Not action planning but movement execution is deficient. *Journal of Autism and Developmental Disorders, 43*(12), 2793–2806. https://doi.org/10.1007/s10803-013-1825-8.

Stone, W. L., Ousley, O. Y., & Littleford, C. D. (1997). Motor imitation in young children with autism: What's the object? *Journal of Abnormal Child Psychology, 25*(6), 475–485. https://doi.org/10.1023/A:1022685731726.

Stone, W. L., & Yoder, P. J. (2001). Predicting spoken language level in children with autism spectrum disorders. *Autism, 5*(4), 341–361. https://doi.org/10.1177/1362361301005004002.

Studenka, B. E., Gillam, S. L., Hartzheim, D., & Gillam, R. B. (2017). Motor and verbal perspective taking in children with autism spectrum disorder: Changes in social interaction with people and tools. *Research in Developmental Disabilities, 66*, 64–79. https://doi.org/10.1016/j.ridd.2017.02.017.

Sumner, E., Leonard, H. C., & Hill, E. L. (2016). Overlapping Phenotypes in Autism spectrum disorder and developmental coordination disorder: A cross-syndrome comparison of motor and social skills. *Journal of Autism and Developmental Disorders, 46*(8), 2609–2620. https://doi.org/10.1007/s10803-016-2794-5.

Supekar, K., & Menon, V. (2015). Sex differences in structural organization of motor systems and their dissociable links with repetitive/restricted behaviors in children with autism. *Molecular Autism, 6*, 50. https://doi.org/10.1186/s13229-015-0042-z.

Sutera, S., Pandey, J., Esser, E. L., Rosenthal, M. A., Wilson, L. B., Barton, M., et al. (2007). Predictors of optimal outcome in toddlers diagnosed with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 37*(1), 98–107. https://doi.org/10.1007/s10803-006-0340-6.

van Swieten, L. M., van Bergen, E., Williams, J. H., Wilson, A. D., Plumb, M. S., Kent, S. W., et al. (2010). A test of motor (not executive) planning in developmental coordination disorder

and autism. *Journal of Experimental Psychology Human Perception and Performance, 36*(2), 493.

Tager-Flusberg, H. (1992). Autistic children's talk about psychological states: deficits in the early acquisition of a theory of mind. *Child Development, 63*(1), 161—172. https://doi.org/10.2307/1130910.

Tager-Flusberg, H., & Sullivan, K. (1994). A second look at second-order belief attribution in autism. *Journal of Autism and Developmental Disorders, 24*, 577—586. https://doi.org/10.1007/BF02172139.

Tager-Flusberg, H., & Sullivan, K. (1995). Attributing mental states to story characters: A comparison of narratives produced by autistic and mentally retarded individuals. *Applied Psycholinguistics*. https://doi.org/10.1017/S0142716400007281.

Takarae, Y., Minshew, N. J., Luna, B., & Sweeney, J. A. (2007). Atypical involvement of frontostriatal systems during sensorimotor control in autism. *Psychiatry Research — Neuroimaging, 156*(2), 117—127. https://doi.org/10.1016/j.pscychresns.2007.03.008.

Teitelbaum, P., Teitelbaum, O., Nye, J., Fryman, J., & Maurer, R. G. (1998). Movement analysis in infancy may be useful for early diagnosis of autism. *Proceedings of the National Academy of Sciences, 95*(23), 13982—13987. https://doi.org/10.1073/pnas.95.23.13982.

Tesink, C. M. J. Y., Buitelaar, J. K., Petersson, K. M., van der Gaag, R. J., Kan, C. C., Tendolkar, I., et al. (2009). Neural correlates of pragmatic language comprehension in autism spectrum disorders. *Brain: A Journal of Neurology, 132*(Pt 7), 1941—1952. https://doi.org/10.1093/brain/awp103.

Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience, 17*, 273—281. https://doi.org/10.1162/0898929053124965.

Thelen, E. (1995). Motor development: A new synthesis. *American Psychologist, 50*(2), 79—95. https://doi.org/10.1037/0003-066X.50.2.79.

Thelen, E. (2005). Dynamic systems theory and the complexity of change. *Psychoanalytic Dialogues: The International Journal of Relational Perspectives, 15*(2), 255—283. https://doi.org/10.1080/10481881509348831.

Thelen, E., & Smith, L. B. (1994). A dynamic systems approach to the development of cognition and action. *Journal of Cognitive Neuroscience, 512*. https://doi.org/10.1162/jocn.1995.7.4.512.

Théoret, H., Halligan, E., Kobayashi, M., Fregni, F., Tager-Flusberg, H., & Pascual-Leone, A. (2005). Impaired motor facilitation during action observation in individuals with autism spectrum disorder. *Current Biology*. https://doi.org/10.1016/j.cub.2005.01.022.

Thompson, A., Murphy, D., Dell'Acqua, F., Ecker, C., McAlonan, G., Howells, H., et al. (2017). Impaired communication between the motor and somatosensory homunculus is associated with poor manual dexterity in autism spectrum disorder. *Biological Psychiatry, 81*(3), 211—219. https://doi.org/10.1016/j.biopsych.2016.06.020.

Thurm, A., Lord, C., Lee, L.-C., & Newschaffer, C. (2007). Predictors of language acquisition in preschool children with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 37*(9), 1721—1734. https://doi.org/10.1007/s10803-006-0300-1.

Toichi, M., & Kamio, Y. (2001). Verbal association for simple common words in high-functioning autism. *Journal of Autism and Developmental Disorders, 31*, 483—490. https://doi.org/10.1023/A:1012216925216.

Toichi, M., & Kamio, Y. (2003). Long-term memory in high-functioning autism: Controversy on episodic memory in autism reconsidered. *Journal of Autism and Developmental Disorders, 33*, 151—161. https://doi.org/10.1023/A:1022935325843.

Tomasello, R., Garagnani, M., Wennekers, T., & Pulvermüller, F. (2016). Brain connections of words, perceptions and actions: A neurobiological model of spatio-temporal semantic activation in the human cortex. *Neuropsychologia*. https://doi.org/10.1016/j.neuropsychologia.2016.07.004.

Tomasello, R., Garagnani, M., Wennekers, T., & Pulvermüller, F. (2017). Brain connections of words, perceptions and actions: A neurobiological model of spatio-temporal semantic activation in the human cortex. *Neuropsychologia, 98*, 111—129.

Tomasello, M., & Kruger, A. C. (1992). Joint attention on actions: acquiring verbs in ostensive and non-ostensive contexts. *Journal of Child Language, 19*(2), 311—333. https://doi.org/10.1017/S0305000900011430.

de la Torre-Ubieta, L., Won, H., Stein, J. L., & Geschwind, D. H. (2016). Advancing the understanding of autism disease mechanisms through genetics. *Nature Medicine, 22*(4), 345—361. https://doi.org/10.1038/nm.4071.

Toth, K., Dawson, G., Meltzoff, A. N., Greenson, J., & Fein, D. (2007). Early social, imitation, play, and language abilities of young non-autistic siblings of children with autism. *Journal of Autism and Developmental Disorders, 37*(1), 145—157. https://doi.org/10.1007/s10803-006-0336-2.

Travers, B. G., Bigler, E. D., Duffield, T. C., Prigge, M. D. B., Froehlich, A. L., Lange, N., et al. (2016). Longitudinal development of manual motor ability in autism spectrum disorder from childhood to mid-adulthood relates to adaptive daily living skills. *Developmental Science*. https://doi.org/10.1111/desc.12401.

Travers, B. G., Bigler, E. D., Tromp, D. P. M., Adluru, N., Destiche, D., Samsin, D., et al. (2015). Brainstem white matter predicts individual differences in manual motor difficulties and symptom severity in autism. *Journal of Autism and Developmental Disorders, 45*(9), 3030—3040. https://doi.org/10.1007/s10803-015-2467-9.

Travers, B. G., Powell, P. S., Klinger, L. G., & Klinger, M. R. (2013). Motor difficulties in autism spectrum disorder: Linking symptom severity and postural stability. *Journal of Autism and Developmental Disorders, 43*(7), 1568—1583. https://doi.org/10.1007/s10803-012-1702-x.

Trumpp, N. M., Traub, F., & Kiefer, M. (2013). Masked priming of conceptual features reveals differential brain activation during unconscious access to conceptual action and sound information. *PLoS One, 8*. https://doi.org/10.1371/journal.pone.0065910.

Trumpp, N. M., Traub, F., Pulvermüller, F., & Kiefer, M. (2014). Unconscious automatic brain activation of acoustic and action-related conceptual features during masked repetition priming. *Journal of Cognitive Neuroscience, 26*, 352—364. https://doi.org/10.1162/jocn_a_00473.

Tschentscher, N., Hauk, O., Fischer, M. H., & Pulvermüller, F. (2012). You can count on the motor cortex: Finger counting habits modulate motor cortex activation evoked by numbers. *NeuroImage, 59*, 3139—3148. https://doi.org/10.1016/j.neuroimage.2011.11.037.

Uljarevic, M., & Hamilton, A. (2013). Recognition of emotions in autism: A formal meta-analysis. *Journal of Autism and Developmental Disorders, 43*(7), 1517—1526. https://doi.org/10.1007/s10803-012-1695-5.

Uljarevic, M., Hedley, D., Alvares, G. A., Varcin, K. J., & Whitehouse, A. J. (2017). Relationship between early motor milestones and severity of restricted and repetitive behaviors in children and adolescents with autism spectrum disorder. *Autism Research, 10*(6), 1163—1168.

Ullman, M. T., & Pierpont, E. I. (2005). Specific language impairment is not specific to language: the procedural deficit hypothesis. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior, 41*(3), 399—433. https://doi.org/10.1016/S0010-9452(08)70276-4.

Vaivre-Douret, L., Lalanne, C., Ingster-Moati, I., Boddaert, N., Cabrol, D., Dufier, J.-L., et al. (2011). Subtypes of developmental coordination disorder: research on their nature and etiology. *Developmental Neuropsychology, 36*(5), 614–643. https://doi.org/10.1080/87565641.2011.560696.

Vanvuchelen, M., Roeyers, H., & De Weerdt, W. (2007). Nature of motor imitation problems in school-aged boys with autism: a motor or a cognitive problem? *Autism: The International Journal of Research and Practice, 11*(3), 225–240. https://doi.org/10.1177/1362361307076846.

Van Waelvelde, H., Oostra, A., Dewitte, G., Van Den Broeck, C., & Jongmans, M. J. (2010). Stability of motor problems in young children with or at risk of autism spectrum disorders, ADHD, and or developmental coordination disorder. *Developmental Medicine & Child Neurology, 52*(8), e174–e178.

Vernazza-Martin, S., Martin, N., Vernazza, A., Lepellec-Muller, A., Rufo, M., Massion, J., et al. (2005). Goal directed locomotion and balance control in autistic children. *Journal of Autism and Developmental Disorders, 35*(1), 91–102. https://doi.org/10.1007/s10803-004-1037-3.

Vigliocco, G., Kousta, S., Della Rosa, P., Vinson, D., Tettamanti, M., Devlin, J., et al. (2014). The neural representation of abstract words: the role of emotion. *Cerebral Cortex, 24*(7), 1767–1777.

Vilensky, J. A., Damasio, A. R., & Maurer, R. G. (1981). Gait disturbances in patients with autistic behavior: a preliminary study. *Archives of Neurology, 38*, 646–649. https://doi.org/10.1001/archneur.1981.00510100074013.

Visser, M., Jefferies, E., & Lambon Ralph, M. A. (2010). Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *Journal of Cognitive Neuroscience, 22*(6), 1083–1094. https://doi.org/10.1162/jocn.2009.21309.

Visser, M., Jeffries, E., Embleton, K. V., & Lambon Ralph, M. A. (2012). Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes. *Journal of Cognitive Neuroscience, 24*(8), 1766–1778.

Vissers, M. E., Cohen, M. X., & Geurts, H. M. (2012). Brain connectivity and high functioning autism: A promising path of research that needs refined models, methodological convergence, and stronger behavioral links. *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2011.09.003.

Vorstman, J. A. S., Parr, J. R., Moreno-De-Luca, D., Anney, R. J. L., Nurnberger, J. I., Jr., & Hallmayer, J. F. (2017). Autism genetics: opportunities and challenges for clinical translation. *Nature Reviews Genetics, 18*(6), 362–376. https://doi.org/10.1038/nrg.2017.4.

Wadsworth, H. M., Maximo, J. O., Lemelman, A. R., Clayton, K., Sivaraman, S., Deshpande, H. D., et al. (2017). The action imitation network and motor imitation in children and adolescents with autism. *Neuroscience, 343*, 147–156. https://doi.org/10.1016/j.neuroscience.2016.12.001.

Wahlberg, T., & Magliano, J. P. (2004). The ability of high function individuals with autism to comprehend written discourse. *Discourse Processes*. https://doi.org/10.1207/s15326950dp3801_5.

Wang, Y., & Hamilton, A. F. (2012). Social Top-down Response Modulation (STORM): A model of the control of mimicry in social interaction. *Frontiers in Human Neuroscience, 6*.

Warren, S. F., Gilkerson, J., Richards, J. A., Oller, D. K., Xu, D., Yapanel, U., et al. (2010). What automated vocal analysis reveals about the vocal production and language learning environment of young children with autism. *Journal of Autism and Developmental Disorders, 40*(5), 555–569. https://doi.org/10.1007/s10803-009-0902-5.

Westermann, G., & Miranda, E. R. (2004). A new model of sesorimotor coupling in the development of speech. *Brain and Language, 89*(2), 393–400.

Whittingham, K., Fahey, M., Rawicki, B., & Boyd, R. (2010). The relationship between motor abilities and early social development in a preschool cohort of children with cerebral palsy. *Research in Developmental Disabilities, 31*(6), 1346–1351. https://doi.org/10.1016/j.ridd.2010.07.006.

Whyatt, C. P., & Craig, C. M. (2012). Motor skills in children aged 7-10 years, diagnosed with autism spectrum disorder. *Journal of Autism and Developmental Disorders, 42*(9), 1799–1809. https://doi.org/10.1007/s10803-011-1421-8.

Wild, K. S., Poliakoff, E., Jerrison, A., & Gowen, E. (2012). Goal-directed and goal-less imitation in autism spectrum disorder. *Journal of Autism and Developmental Disorders, 42*(8), 1739–1749. https://doi.org/10.1007/s10803-011-1417-4.

Willems, R. M., Peelen, M. V., & Hagoort, P. (2010). Cerebral lateralization of face-selective and body-selective visual areas depends on handedness. *Cerebral Cortex, 20*, 1719–1725. https://doi.org/10.1093/cercor/bhp234.

Williams, J. H. G. (2008). Self-other relations in social development and autism: Multiple roles for mirror neurons and other brain bases. *Autism Research*. https://doi.org/10.1002/aur.15.

Williams, J. H. G., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/S0149-7634(01)00014-00018.

Wilson, P. H., & McKenzie, B. E. (1998). Information processing deficits associated with developmental coordination disorder: A meta-analysis of research findings. *Journal of Child Psychology and Psychiatry, 39*(6), 829–840. https://doi.org/10.1111/1469-7610.00384.

Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nature Neuroscience, 7*, 701–702. https://doi.org/10.1038/nn1263.

Wing, L. (1981). Language, social, and cognitive impairments in autism and severe mental retardation. *Journal of Autism and Developmental Disorders, 11*, 31–44. https://doi.org/10.1007/BF01531339.

Wing, L., & Gould, J. (1979). Severe impairments of social interaction and associated abnormalities in children: Epidemiology and classification. *Journal of Autism and Developmental Disorders, 9*(1), 11–29. https://doi.org/10.1007/BF01531288.

Wing, L., Gould, J., & Gillberg, C. (2011). Autism spectrum disorders in the DSM-V: Better or worse than the DSM-IV? *Research in Developmental Disabilities, 32*(2), 768–773. https://doi.org/10.1016/j.ridd.2010.11.003.

Wittgenstein, L. (1953). *Philosophical investigations* (Vol. 1999/1967). Oxford Blackwell. Retrieved from: http://books.google.com.au/books?hl=en&lr=&id=JoPYriJM1cwC&oi=fnd&pg=PA20&dq=Wittgenstein&ots=5uDSJTF6j5&sig=fHuLfYMHNU4iZlPMnEasWEQjgGo.

Wood, A., Rychlowska, M., Korb, S., & Niedenthal, P. (2016). Fashioning the face: sensorimotor simulation contributes to facial expression recognition. *Trends in Cognitive Sciences, 20*(3), 227–240.

Yang, D. Y.-J., Rosenblau, G., Keifer, C., & Pelphrey, K. A. (2015). An integrative neural model of social perception, action observation, and theory of mind. *Neuroscience and Biobehavioral Reviews, 51*, 263–275. https://doi.org/10.1016/j.neubiorev.2015.01.020.

Yingling, J. (1981). *Temporal features of infant speech: A description of babbling patterns circumscribed by postural achievement*. Unpublished doctoral dissertation. University of Denver.

Yirmiya, N., Kasari, C., Sigman, M., & Mundy, P. (1989). Facial expressions of affect in autistic, mentally retarded and normal

children. *Journal of Child Psychology and Psychiatry, and Allied Disciplines, 30*(5), 725—735. https://doi.org/10.1111/j.1469-7610.1989.tb00785.x.

Young, R. L., Brewer, N., & Pattison, C. (2003). Parental identification of early behavioural abnormalities in children with autistic disorder. *Autism, 7*(2), 125—143. https://doi.org/10.1177/1362361303007002002.

Ypma, R. J. F., Moseley, R. L., Holt, R. J., Rughooputh, N., Floris, D. L., Chura, L. R., et al. (2016). Default mode hypoconnectivity underlies a sex-related autism spectrum. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging, 1*(4), 364—371. https://doi.org/10.1016/j.bpsc.2016.04.006.

Zaki, J., Weber, J., Bolger, N., & Ochsner, K. (2009). The neural bases of empathic accuracy. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 11382—11387. https://doi.org/10.1073/pnas.0902666106.

Zappella, M., Einspieler, C., Bartl-Pokorny, K. D., Krieber, M., Coleman, M., Bölte, S., et al. (2015). What do home videos tell us about early motor and socio-communicative behaviours in children with autistic features during the second year of life - An exploratory study. *Early Human Development, 91*(10), 569—575. https://doi.org/10.1016/j.earlhumdev.2015.07.006.

Zelaznik, H. N., & Goffman, L. (2010). Generalized motor abilities and timing behavior in children with specific language impairment. *Journal of Speech, Language, and Hearing Research, 53*(2), 383—393. https://doi.org/10.1044/1092-4388(2009/08-0204) (Generalized).

Zwaigenbaum, L., Bryson, S., Rogers, T., Roberts, W., Brian, J., & Szatmari, P. (2005). Behavioral manifestations of autism in the first year of life. *International Journal of Developmental Neuroscience, 23*(2—3 SPEC. ISS.), 143—152. https://doi.org/10.1016/j.ijdevneu.2004.05.001.