



## Early human motor development: From variation to the ability to vary and adapt



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### ABSTRACT

This review summarizes early human motor development. From early fetal age motor behavior is based on spontaneous neural activity: activity of networks in the brainstem and spinal cord that is modulated by supraspinal activity. The supraspinal activity, first primarily brought about by the cortical subplate, later by the cortical plate, induces movement variation. Initially, movement variation especially serves exploration; its associated afferent information is primarily used to sculpt the developing nervous system, and less to adapt motor behavior. In the next phase, beginning at function-specific ages, movement variation starts to serve adaptation. In sucking and swallowing, this phase emerges shortly before term age. In speech, gross and fine motor development, it emerges from 3 to 4 months post-term onwards, i.e., when developmental focus in the primary sensory and motor cortices has shifted to the permanent cortical circuitries. With increasing age and increasing trial-and-error exploration, the infant improves its ability to use adaptive and efficient forms of upright gross motor behavior, manual activities and vocalizations belonging to the native language.

### 1. Introduction

Infancy is characterized by a dramatic increase of motor abilities: the infant learns to reach and grasp, to sit, stand and walk, and to chew and talk. Initially it was thought that these developmental changes were caused by an evolution from infantile reflexes to cortically controlled behavior (Peiper, 1963). But during the last four decades two things became clear: (1) motor behavior is not primarily organized in terms of reflexes; and (2) already at fetal age the cortex is involved in modulating motor behavior (Hadders-Algra, 2018). Motor behavior is especially based on spontaneous, patterned activity, which is a quintessential feature of neural tissue (Blankenship and Feller, 2010; Moore et al., 2011; Raichle, 2015; Ren and Greer, 2003). This implies that motor behavior may emerge in the absence of a sensory stimulus. Motor behavior is the net product of continuous interaction of multiple networks in which various neural pathways may mediate a motor action. A good example of how motor control is organized is the control of rhythmical movements like locomotion, respiration, sucking and mastication. The control of these movements is based on so-called Central Pattern Generators (CPGs). CPGs are neural networks - usually located in the spinal cord or brain stem - which are able to coordinate autonomously, i.e., without segmental sensory or supraspinal information, the activity of many muscles (Frigon, 2017; Grillner et al., 2005). Of course, in typical conditions the CPG network does not work

autonomously, but is affected by segmental afferent signals and by information from cortical-subcortical circuitries. Activity in the latter circuitries is organized in large-scale networks, in which cortical areas are functionally connected through direct recursive interaction or through intermediary cortical or subcortical (striatal, cerebellar) structures (Bassett et al., 2015; Fuertinger et al., 2015). The cortical-subcortical networks expanded substantially during phylogeny and determine to a large extent human motor ontogeny.

During the last decades scientists have succeeded in better and more detailed descriptions of observable changes occurring during early motor development. However, how these developmental changes are brought about by the nervous system is less well understood. This knowledge gap has induced a wealth of theoretical models explaining the developmental mechanisms of motor development. During a major part of the past century the Neural Maturationist Theories guided developmental thinking (e.g., Peiper, 1963). These theories considered motor development basically as an innate, maturational process. But during the last two decades of the previous century it became clear that motor development is largely affected by experience. Currently, two theoretical frameworks are dominant, the Dynamic Systems Theory (DST; Smith and Thelen, 2003; Spencer et al., 2011; Thelen, 1995; Ulrich, 1997) and the Neuronal Group Selection Theory (NGST; Edelman, 1989, 1993; Hadders-Algra, 2000, 2010). These frameworks share the opinion that motor development is a non-linear process with

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phases of transition, a process which is affected by many factors. The factors consist of features of the child itself, such as body weight, muscle power, or the presence of a cardiac disorder, and components of the environment, such as housing conditions, the composition of the family, and the presence of toys. In other words, both theories acknowledge the importance of experience and context. But the two theories differ in their opinion on the role of genetically determined neurodevelopmental processes. Genetic factors only play a limited role in DST, whereas in NGST genetic information, epigenetic cascades and experience play equally prominent roles (NGST; Edelman, 1989, 1993; Hadders-Algra, 2000, 2010). As the latter corresponds better to current insights in the complexities of genetic and epigenetic control of neural development (Kang et al., 2011; Lv et al., 2013; Spitzer, 2006), I will use the NGST as reference framework. Key notions in the NGST are variation, i.e., the presence of a repertoire of options to achieve a specific goal, and adaptability, i.e., the capacity to select from the repertoire the most efficient strategy in a specific situation (Hadders-Algra, 2000, 2010; Edelman, 1993).

The aim of this paper is to review early human motor development, i.e., motor development during fetal life and the first two postnatal years. The review underlines that the age of 3 months post-term – or rather the period between 2 and 4 months – is an age of major transition in motor development (Hadders-Algra, 2018; Prechtel, 1984). By and large, it consists of the transition from endogenously generated varied movements that primarily serve exploration and sculpting of the nervous system, to movements that increasingly better can be varied and adapted to the constraints of the environment. The development of sucking and swallowing forms an exception to this general rule of transition: it is adaptive from 36 weeks postmenstrual age (PMA) onwards.

Before presenting the specifics of motor behavior during early life, I will first address general characteristics of motor development taking the NGST as frame of reference. Next, I will discuss the general movements, the principal motor behavior of early life. Subsequent sections review the general principles of development of goal directed motor behavior: gross motor development (Section 4), fine motor development (Section 5) and oral motor development (Section 6).

## 2. Neuronal group selection theory: variation and ability to vary and adapt

NGST's starting point is the variation in neural behavior (Changeux, 1997; Chervyakov et al., 2016; Edelman, 1989, 1993). According to NGST, motor development is characterized by two phases of variability: primary and secondary variability (Edelman, 1989). The borders of variability are determined by genetic instructions (Chervyakov et al., 2016; Krubitzer and Kaas 2005). Development starts with the phase of primary variability during which the spontaneous activity of the nervous system tries out all available functional options (Leighton and Lohmann, 2016). In terms of motor behavior, this means that the nervous system explores all motor possibilities of its repertoires therewith inducing abundant variation in motor behavior (Hadders-Algra 2000, 2010). The varied exploration generates a wealth of self-produced afferent information, which in turn is used directly or indirectly via transcriptional gene expression for further shaping of the nervous system (experience-expectant development; Greenough et al., 1987). However, initially, i.e., during the phase of primary variability, the afferent information can only be used to a limited extent to adapt motor behavior to the specifics of the situation. The ample spontaneous activity especially prepares the nervous system for the accurate and integrated use of afferent, perceptual information to adapt motor behavior in a later phase (Leighton and Lohmann, 2016). For instance, the spontaneous motor behavior assists the fine-tuning of the genetically based structure of the somatosensory cortex (Florence et al., 1996; Khazipov et al., 2004). To summarize the above, in the phase of primary variability motor behavior is characterized by variation with no

or marginal adaptation (Hadders-Algra 2010).

At a certain point in time, the phase of secondary or adaptive variability starts. In this phase the nervous system clearly uses the afferent information produced by behavior and experience for selection of the motor behavior which fits the situation best (Edelman, 1989; Hadders-Algra et al., 1996a, 2010). The process of selection, which is characteristic of secondary variability, is based on active trial and error experiences (experience-dependent development; Edelman, 1993; Greenough et al., 1987; Takahashi et al., 2013). This means that spontaneous, i.e., self-produced, motor behavior with its associated sensorimotor experience plays a pivotal role in motor development (Adolph, 1997; Adolph and Franchak, 2017; Bertenthal et al., 1994; Cole et al., 2016; Hadders-Algra et al., 1996a; Higgins et al., 1996). Sensorimotor experience involves multimodal information, that is, the joint information from multiple sensory systems, such as the proprioceptive, haptic, visual and auditory systems.

To determine the nature of the most adaptive behavior specific reference values are used. The well-studied development of song in birds may serve as a case in point. Juvenile zebra finches learn to select specific adult song patterns – the local dialect – from their inherited varied vocal repertoire by listening to, memorizing and practicing the song of a tutor, typically their father (Marler and Tamura, 1964; Olson et al., 2015; Olveczky and Gardner, 2011). Another example is the way in which sitting infants, whose balance is perturbed, learn to select the most adaptive postural adjustment from their repertoire; this selection is guided by information on the stability of the head during the postural perturbation (Hadders-Algra et al., 1996b).

The process of motor learning and selection from the repertoire is especially effective when the infant engages in play with others, e.g., caregivers or siblings. The infant does not only learn from its own trial and error attempts, but the infant also profits from the actions performed by others due to the neural mirroring mechanisms (Meltzoff et al., 2009). These mechanisms are already present in newborn infants, be it to a limited extent (Burzi et al., 2015; Meltzoff et al., 2017). During the first postnatal year, the mirroring capacities get increasingly tuned to the actions of others (Natale et al., 2014; Turati et al., 2013). The tuning is sculpted by experience: the mirror networks respond in particular to actions that infants have experienced themselves (Rotem-Kohavi et al., 2014). Infants profit especially from the observation of others' actions when infant and partner are involved in mutual imitative play, a profit that increases in the beginning of the second postnatal year (Agnetta and Rochat, 2004; Marshall and Meltzoff, 2014).

The process of selection and learning the most adaptive motor behavior, occurs at various levels of neural organization. At cellular level selection is mediated by changes in synaptic strength in which the topology of the cells (Nelson et al., 1993), selection and reorganization of dendritic spines (Kasai et al., 2010; Xu et al., 2009) and the presence or absence of coincident electrical activity in pre- and postsynaptic neurons play a role (Changeux and Danchin, 1976; Di Filippo et al., 2009; Hebb, 1949). In terms of the organization of motor control, selection occurs at the level of neural coalitions, i.e., selection of the most efficient motor strategy. This is reflected in the temporal and quantitative tuning of motor output. Recent neurophysiological data of animal studies that recorded neural activity during motor learning indicated that the basal ganglia in collaboration with cortico-limbic circuitries may play a major role in the selection of motor strategies, i.e., in motor sequence learning (Gurney et al., 2015; Shipp, 2017; Smith and Graybiel, 2014; Stephenson-Jones et al., 2013), whereas the cerebellum may be the key-structure involved in the selection of situation specific temporal and quantitative parameters of motor output, i.e., in the fine-tuning of motor adaptation, for instance by adaptation of the timing or the degree of muscle contraction (Taylor and Ivry, 2014).

The transition from primary to secondary variability occurs at function-specific ages (Hadders-Algra 2000, 2010; Heineman et al., 2010). For instance, in the development of sucking behavior the phase

of secondary variability starts prior to term age (Vice and Gewolb, 2008), in the development of postural adjustments it emerges after the age of 3 months (De Graaf-Peters et al., 2007; Hedberg et al., 2005), in arm movements during reaching between 6 and 15 months (Heineman et al., 2010), and in the development of foot-placing during walking it starts between 12 and 18 months (Cioni et al., 1993). This also means that the phase of secondary variability starts at an age at which the processing of sensory information has not achieved its final, accurate, adult stage. Interestingly, computer models suggest that the initial phases of motor learning are more effective when feedback is received from low resolution sensory systems, i.e., systems that do not supply clear but rather imprecise information, than when the feedback is provided by full resolution systems that furnish accurate information (Jacobs and Dominguez, 2003).

The age at which adaptive behavior first can be observed depends on the method of investigation. For instance, with the application of electromyographic (EMG) recordings the first signs of adaption in postural behavior during sitting may be observed at the age of 4 months (Hedberg et al., 2005), but when simple behavioral observation is used signs of adaptive sitting behavior are first detected from 6 months onwards (Heineman et al., 2010). In the second half of the second post-natal year all basic motor functions, such as sucking, reaching, grasping, postural control and locomotion, have reached the first stages of secondary variability. It takes however until late adolescence before the secondary neural repertoire has obtained its adult configuration (Hadders-Algra, 2010).

The protracted course of the development of secondary variability is brought about by the long lasting developmental processes in the brain, such as dendritic refinement, myelination, and extensive synapse rearrangement (De Graaf-Peters and Hadders-Algra, 2006). The developmental changes result in newly emerging neural coalitions that allow for the selection of increasingly complex movement sequences, such as involved in playing the piano, dancing Tchaikovsky's Swan Lake, or performing a Cassina-Kovacs-Kolman combination on the high bar. Finally, the young adult is equipped with a varied movement repertoire with multiple efficient and preprogrammed motor solutions for commonly encountered situations, and one specific, optimal solution for high constraint situations. The repertoire also allows for ongoing exploration of new coalitions by means of imitation and trial and error; this ability to vary paves the way for the creative attainment of new motor actions, and the collection of perceptual, cognitive and social information (cf., Orth et al., 2017).

The varied nature of the nervous system and its continuous interaction with varied environments gives rise to abundant diversity in the way motor development presents in individual children. Motor development is not only characterized by variation in the way tasks may be accomplished (on the basis of the repertoire available), but also by intra- and inter-individual variants in the speed in which developmental milestones are achieved. As a result, the ages at which motor milestones are reached, are widely scattered – also across cultures (Mendonça et al., 2016; WHO Multicentre Growth Reference Study Group, 2006) - a diversity that grows with increasing age (Fig. 1). The cultural variation in the development of independent sitting was elegantly demonstrated by the study of Karasik et al. (2015). It evaluated sitting behavior of 5-month-old infants in the home situation during natural daily activities in six countries. The study showed that none of the Italian infants could sit independently, 17% to 25% of infants from the USA, South Korea and Argentina, and 67% of Kenyan infants, and 92% of Cameroonian infants (Karasik et al., 2015). The differences in sitting capacities were associated with different experiences of the infants: infants from the first four countries spent little or no time on the ground or on adult furniture, whereas infants from Kenya and Cameroon spent most of their sitting times in these contexts.

The variation in the development of motor milestones includes the co-occurrence of different developmental phases. For instance, infants may switch back and forth from belly crawling to crawling on hands

and knees (Adolph et al., 1998; McGraw, 1943; Touwen, 1976). Typically developing infants may also exhibit a temporary regression, an 'inconsistency', in the development of a specific function (Touwen, 1976). As long as the regression is restricted to a single function, it can be regarded as another expression of developmental variation. The large variation in the attainment of milestones (Fig. 1) implies that delayed development of a single milestone has limited clinical value. However, delay in the attainment of multiple milestones suggests an increased risk of developmental pathology (Petersen et al., 1998).

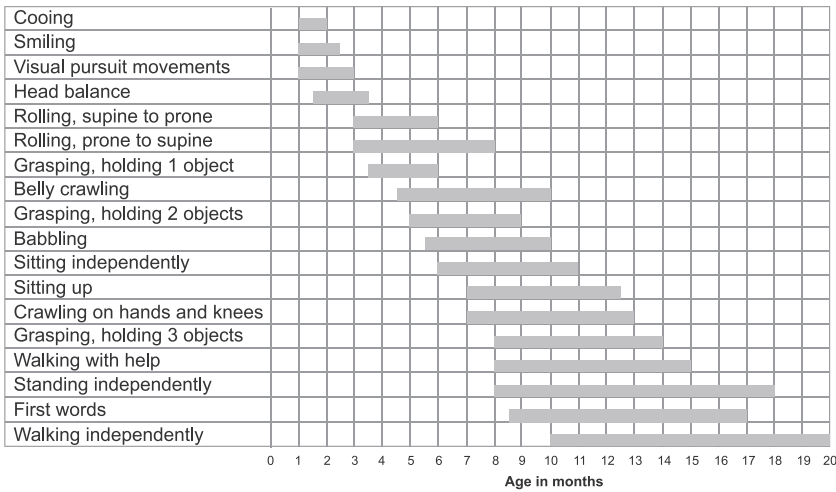
### 3. General movements: cornerstone of early motor development

A vaginal ultrasound study showed that the first human fetal movements emerge at the age of 7 weeks and 2 days PMA (Lüchinger et al., 2008). They consist of slow, small sideways bending movements of head and/or trunk. A few days later, these simple movements develop into movements in which also one or two arms or legs participate. The emergence of the first fetal movements at week 7 PMA corresponds to the development of synapses in the spinal cord, a process that begins in week 6 and accelerates in week 7 PMA (Okado, 1980), and to the emerging neuromuscular contacts (Altman and Bayer, 2001). The first fetal movements develop before the spinal reflex pathways are completed. The latter emerge at week 10–11 PMA (Clowry et al., 2005). This underlines the endogenous or spontaneous generation of early motor activity. The first movements of all body parts are slow, small, simple and stereotyped (Lüchinger et al., 2008) and have the appearance of the generalized motility of the chick embryo (Hamburger, 1973). At 9–10 weeks PMA general movements (GMs) emerge, i.e., movements in which all parts of the body participate and during which movement direction, amplitude and speed varies. Similar complex and varied GMs have also been observed in the fetal guinea pig (Van Kan et al., 2009). During GMs all possible combinations of degrees of freedom in the various body joints are explored. GMs are the example par excellence of motor behavior during the phase of primary variability. Interestingly, the emergence of varied and complex GMs at 9–10 weeks PMA coincides with the appearance of neurons with synaptic vesicles suggestive of synaptic activity in the cortical subplate (Molliver et al., 1973; Supèr et al., 1998).

GMs continue to be present throughout pregnancy and during the first months after term age (Fig. 2). In fact, GM-activity is the most prevalent type of motor behavior of the fetus and young infant (De Vries et al., 1982; Hadders-Algra, 2004). GMs are characterized by a large variation in muscle activity, but also by high degrees of antagonistic co-activation (Hadders-Algra et al., 1997). Prior to 36–38 weeks PMA the varied and complex GMs included many trunk movements (fetal and preterm GMs; Hadders-Algra, 2007). At 36–38 weeks PMA a transition occurs, the preterm GMs change into the more forceful 'writhing' GMs, in which the trunk participates less obviously than during the preterm phase (Hadders-Algra et al., 1997). At the age of 6–8 weeks post-term GMs change again: the long strokes of the writhing GMs change into the pizzicato movements of 'fidgety' GMs. Fidgety GMs consist of a continuous stream of tiny, elegant movements occurring irregularly all over the body (Precht and Hopkins, 1986; Hadders-Algra and Precht, 1992). The fidgety GMs are most prominently present between 11 and 16 weeks post-term to disappear around 5 months post-term (Ferrari et al., 2016). They are gradually replaced by goal-directed movements, such as mutually manipulative finger movements and reaching movements (Hopkins and Precht, 1984).

Three observations inspired the hypothesis that the varied and complex GMs initially result from activity of the subplate, that modulates the basic activity of the CPG-networks of the GMs in the spinal cord and brain stem (Hadders-Algra, 2007, 2018): (1) the firm body of evidence that GMs with reduced variation and complexity are strongly associated with cerebral palsy (Bosanquet et al., 2013; Einspieler et al., 2005; Hadders-Algra, 2004); (2) the coincidence of the emergence of GM-activity with the emergence of synaptic activity in the cortical





**Fig. 1.** Schematic representation of the ages at which some motor skills emerge during infancy. The length of the bars reflects the inter-individual variation. Adapted from the study of Touwen carried out in the Netherlands in the seventies of last century (Touwen, 1976). Note that the Dutch data are not identical to those of the WHO Multicentre Growth Reference Study Group (2006).



**Fig. 2.** Example of general movement activity in an infant aged 3 months post-term. The frames have been sampled from a video-recording of about 2 min; the frames have an interval of about 5 s. The figure has been produced with permission of the parents.

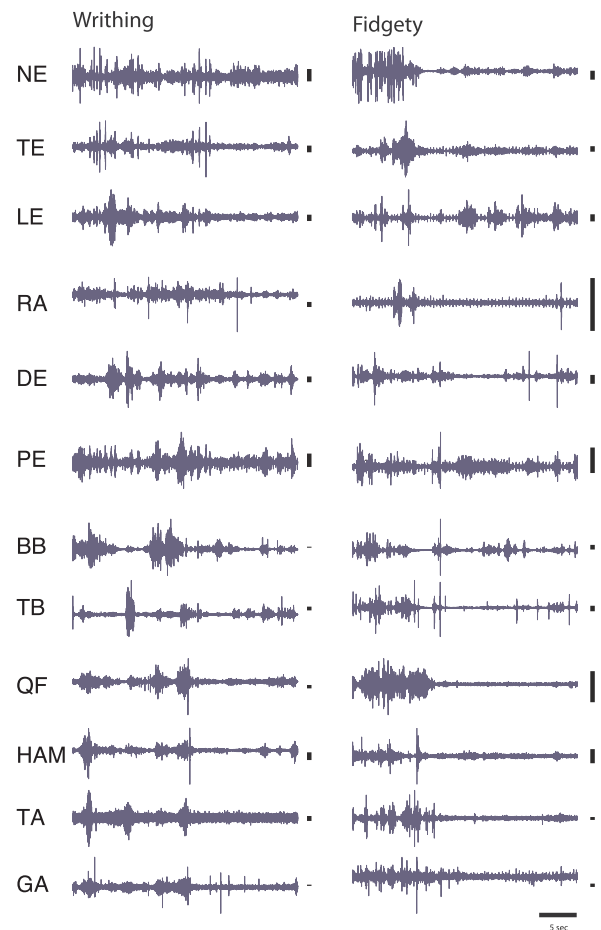
subplate; and (3) the observation that the evolution and transient nature of the subplate matches that of GM-development. The modulating activity is considered to be brought about by the waxing and waning waves of spontaneous activity in the subplate networks involving many neurons with high level activity (Leighton and Lohmann, 2016).

The hypothesis presupposes that the subplate has projections which may directly or indirectly transmit the modulating information to the basic GM-networks in the spinal cord and brain stem. However, evidence that these projections exist is limited, as few studies addressed descending projections of the subplate. Nevertheless, some information is available. First, in the cat subplate afferents have been demonstrated that traverse the internal capsule, invade the thalamus, and project to at least one other subcortical target, i.e., the superior colliculus, at embryonic day 30 (McConnell et al., 1989). Using the neuroinformatics model of Workman and colleagues (Workman et al., 2013), the feline stage of brain development at embryonic day 30 would correspond to the stage of human brain development of approximately 9–10 weeks PMA. Second, studies in the fetal rat indicated that descending supraspinal pathways emerge prior to and coincident with the emergence of subplate neurons at embryonic day 16 (De Boer-van Huizen and Ten Donkelaar et al., 1999; Baislev et al., 1996; Lakke, 1997). Thus, it is conceivable that the subplate induces movement complexity and variation and that this information is transmitted initially via polysynaptic pathways that are present around 9–10 weeks PMA (Luo et al., 1992) to the central pattern generator networks in the brainstem and spinal cord (Kostović and Judas, 2007; Marín-Padilla, 2014). When the subplate gradually dissolves between 3 months before term and 3 months corrected age (CA) the cortical plate in the primary sensorimotor cortices takes over the modulating activity involved in movement complexity and variation ('subplate and cortical plate modulation hypothesis'; Hadders-Algra, 2018).

Network development and increasing thalamo-cortical and cortico-cortical afferent input results in 'sparsification' of activity in the cortical networks, i.e., activity that is less intensive and occurs in more limited groups of neurons (Leighton and Lohmann, 2016; Rochefort et al., 2009). However, in the peri-term period the 'sparsification' is not expressed in motor behavior, presumably due to the transient over-expression of the noradrenergic  $\alpha_2$ - and glutamatergic NMDA receptors and the relatively high serotonergic innervation and dopamine turnover (De Graaf-Peters and Hadders-Algra, 2006; McDonald and Johnston, 1990). It is conceivable that this transient neurotransmitter and receptor configuration is the brain correlate of the increased motoneuronal excitability and the forceful character of the writhing GMs observed during the peri-term period (Hadders-Algra et al., 1992, 1997; Hakamada et al., 1988). After the disappearance of the neural 'hyperexcitability' the sparsification of spontaneous activity in the cortical plate of the primary sensorimotor cortices is expressed in the tiny fidgety movements that occur all over the body ('sparsification hypothesis'; Hadders-Algra, 2018). The fragmentation of motor output is well mirrored in the increasingly smaller bursts of activity in EMG-recordings of GMs (Fig. 3; Hadders-Algra et al., 1997). The emergence of the fidgety movements signals that the nervous system is increasingly prepared to make sense of its own actions and of the environment (Leighton and Lohmann, 2016). It is also the phase that functional connections between corticospinal tract fibers and spinal motoneurons show signs of activity-dependent reorganization (Ritterband-Rosenbaum et al., 2017). In short, the nervous system is ready for full engagement in goal directed motor activities.

#### 4. Gross motor development

Gross motor function comprises the ability to maintain body position and to move around by changing body position or location. This implies that postural control plays a pivotal role. Postural control primarily aims at the maintenance of a vertical posture of head and trunk



**Fig. 3.** Surface EMG-activity during GMs of the same child. On the left during writhing GMs; on the right during fidgety GMs. The developmental changes reflect the sparsification, i.e., the bursts of shorter duration and smaller amplitude during the fidgety GMs. The sparsification does not mean that longer lasting and more intensive EMG-activity is absent from the EMG; it is only the basic melody of movements that obtains the characteristics of sparsification. BB = biceps brachii, DE = deltoid muscle, GA = gastrocnemius, HAM = hamstrings, LE = lumbar extensor, NE = neck extensor, PE = pectoralis major, QU = quadriceps femoris, RA = rectus abdominis, sec = seconds, TA = tibialis anterior, TB = triceps brachii, TE = thoracic extensor. The vertical bars denote 50  $\mu$ V.

against the forces of gravity, as this creates an optimal situation for vision and goal-directed motility (Massion, 1998).

##### 4.1. Development of postural control

Before birth, little postural control is required. The fetus floats in the amniotic fluid, and the uterine walls provide ample support, in particular during the last phases of pregnancy. Postnatally, the situation changes: the all-round support is missing and the infant is exposed to the forces of gravity. When infants are born preterm, the extra-uterine environment induces a change in the varied postures of the limbs: the flexion postures which are most commonly observed in utero (Ververs et al., 1998) change in preterm infants younger than 32 weeks PMA into more or less extended postures. From 32 weeks onwards, the preference for extension changes into a preference for flexion, at first in the legs, and from about 36 weeks onwards also in the arms (Dubowitz et al., 1999). The preference for flexion postures gradually decreases after term age, somewhat earlier in the arms than in the legs (McGraw 1943; Touwen 1976). At 2–3 months post-term the limbs no longer show a particular preference posture. It should be realized that the age-dependent preference postures can be only observed during the relatively

short periods with quiet wakefulness and not during active wakefulness and sleep (Cioni and Prechtl, 1990; Prechtl et al., 1979; Vles et al., 1989). Moreover, recall that the dominant motor behavior of the young infant is not the maintenance of a specific posture, but the exploration of movements by means of varied GMs.

According to Amiel-Tison and Saint-Anne Dargassies antigravity postural control of the neck and trunk is lacking before 32 weeks PMA (Amiel-Tison, 1968; Saint-Anne Dargassies, 1974). Thereafter some head control develops, so that at term age low risk preterm infants, like full-term infants, can keep the head upright for a few seconds while in a sitting position (Dubowitz et al., 1999; Prechtl, 1977). During the following 3 months, infants learn to stabilize the head on the trunk (Lima-Alvarez et al., 2014).

In the following months postural skills rapidly improve. This is reflected by the development of the ability to sit independently around 5–8 months, to stand without support at 9–13 months and to walk independently at 10–14 months (10–90 percentile ranges of the WHO Multicentre Growth Reference Study Group (2006)).

The co-ordination of muscle activity for postural control occurs at two functional levels (CPG-model; Forssberg and Hirschfeld, 1994). The basic level deals with the so-called direction-specificity of the adjustments: during forward body sway the dorsal muscles are primarily recruited, during backward sway the ventral muscles. At the second level of control, the direction-specific adjustments are fine-tuned to the specifics of the situation (Hadders-Algra, 2008). Fine-tuning may be achieved in multiple ways, e.g., by selection of specific direction-specific muscles or by selection of a specific recruitment order (top-down or bottom-up; Hadders-Algra, 2008).

The study of Hedberg et al. (2004), that evaluated postural adjustments in infants during external balance perturbation in sitting position, demonstrated that infants can recruit already at the age of one month direction-specific adjustments. This suggests that the basic level of postural control has an innate origin. The study indicated that the adjustments are not triggered by vestibular information, but most likely by a combination of tactile and proprioceptive information from the supporting pelvic region. The direction-specific adjustments of young infants are characterized by abundant variation, e.g., in the participating direction-specific muscles, their timing, and in the participation of antagonist muscles, reflecting the phase of primary variability. From the age of 4 months onwards secondary variability starts: the infants gradually learn to select the adjustment that is most appropriate for the situation (Hedberg et al., 2005). Selection is clearly activity-dependent; it is based on trial and error learning (Hadders-Algra et al., 1996a). Selection occurs first in terms of which muscles are recruited (Hadders-Algra et al., 1996b; Hedberg et al., 2005). Next, from about the age of 9 months also the timing and degree of muscle contraction are increasingly used to adapt posture (Van Balen et al., 2012; Van der Fits et al., 1999a). Meanwhile the infant learns to sit independently. Centre of pressure recordings indicated that the emergence of the ability to sit independently is accompanied by selection of a specific set of postural behaviors, which is temporarily mediated by freezing of the degrees of freedom (Kyvelidou et al., 2013). The latter is a well-known strategy to simplify control, especially in high constraint conditions (Bernstein, 1935). A similar temporarily freezing of the degrees of freedom is not observed in all sitting conditions, for instance not during reaching while sitting in a supportive infant chair (Boxum et al., 2014).

The development of the ability to stand independently is associated with an increasing selection of direction-specific activity in the ankle muscles during standing (Hedberg et al., 2007). The phase of learning to stand and walk, which is characterized by integration of new sensory, e.g., haptic and proprioceptive, information (Barela et al., 1999; Chen et al., 2016), is also associated with a temporarily freezing of degrees of freedom (Assaiante, 1998). This is associated with selection of the direction-specific adjustment in which all direction-specific neck and trunk muscles are recruited (*en bloc* strategy). The dominant presence of the *en bloc* strategy in challenging balance situations starts around 9

months and lasts until the age of about 2.5 years. After 2.5 years, the energy consuming *en bloc* strategy gives way to a varied use of adjustments that involve the activation of less direction-specific muscles (Hadders-Algra et al., 1996b, 1998).

Anticipatory postural adjustments emerge around 2 months post-term: 2-month-olds show minor anticipatory postural adjustments of arms and legs when their mother picks them up from lying in supine position. The anticipatory adjustments to these ‘pick-ups’ rapidly improve at 3–4 months (Reddy et al., 2013). Anticipatory postural adjustments during reaching in supported sitting are inconsistently present from 4 months onwards (Van Balen et al., 2012), but anticipatory adjustments especially increase during the first months of walking independently - an activity that challenges the use of anticipatory postural activity (Barela et al., 1999; Cignetti et al., 2013). The degree of postural practice and challenge experienced by novice walkers was assessed by Adolph and colleagues: they estimated that early walkers generate about 14,000 steps and 100 falls per day (Adolph et al., 2012).

The fine-tuning of postural adjustments is not completed after some months of walking experience; it takes until the age of about 18 years to establish the adult capacity to modulate the temporal and quantitative parameters of postural adjustments (Barlaam et al., 2012).

#### 4.2. Development of locomotor behavior

In the fetus locomotive leg movements have been described from 14 weeks PMA onwards (Birnholtz et al., 1978; De Vries et al., 1984). At birth, the infant shows locomotor-like behavior in the form of neonatal stepping movements (Forssberg, 1985). Neonatal stepping movements have been reported in preterm infants, but prior to 36 weeks PMA, i.e., the age of the emergence of the neural ‘hyperexcitability’ (Herlenius and Lagercrantz, 2010), they are rather hard to elicit (Thelen and Cooke, 1987). The varied stepping movements are characterized by synchronized hyperflexion of the hips and knees and high degrees of antagonistic co-activation of the leg muscles (Forssberg, 1985). The stepping movements are probably the result of activity of a spinal CPG-network that is modulated by supraspinal activity (Lacquaniti et al., 2012), analogous to the neural substrate of GMs. The presence of a spinal locomotor CPG has been demonstrated in the hindlimbs of kittens after a transection of the thoracic cord; the spinal CPG is also considered to be the substrate of the locomotor-like activity in persons with a spinal cord injury (Dietz et al., 1994; Forssberg, 1985; Yang and Gorassini, 2006). The EMG-studies of Lacquaniti and co-workers, during which twenty four leg and trunk muscles were recorded simultaneously, showed that neonatal stepping is characterized by two EMG-patterns: one assisting body support during stance, the other helping to drive the limb during swing (Lacquaniti et al., 2012). In the absence of specific training or of support by water buoyancy (Thelen and Cooke, 1987), the stepping movements disappear around the age of 2–3 months (Forssberg, 1985) – a disappearance that may be related to the disappearance of the perinatal neural ‘hyperexcitability’ (Herlenius and Lagercrantz, 2010). However, when neonatal stepping is trained daily, the stepping response can be elicited until its replacement by supported locomotion. Training of stepping movements is associated with an acceleration of the ability to walk independently of four to six weeks (Zelazo et al., 1972). However, typically, i.e., without training, a period of locomotor silence follows after the age of 2–3 months.

The locomotor silence does not imply that the infant stops with gross motor activity. From 4–5 months onwards infants start to explore rolling movements, from supine to prone and vice versa, and in prone they explore goal directed progression. The transition to progression in prone is associated with changes in social-emotional development (e.g., becoming more autonomous and more sensitive to maternal separations), increased referential gesture communication, and spatial abilities, including the onset of wariness of heights (Anderson et al., 2013; Campos et al., 2000). During belly crawling many variants are tried out (Fig. 4; Adolph et al., 1998; Freedland and Bertenthal, 1994; Largo et al.



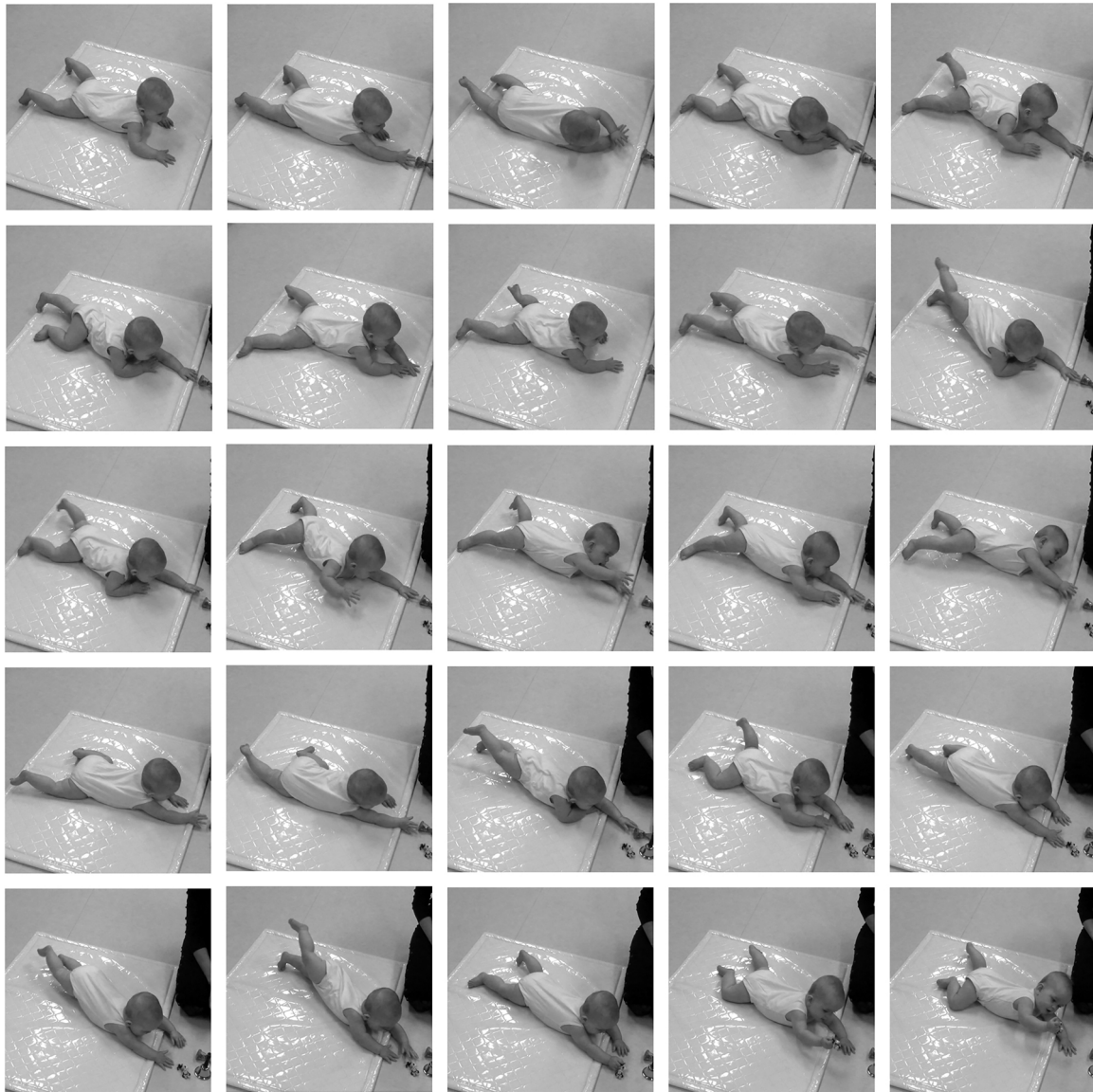


Fig. 4. Example of the varied exploration of movements during the early phases of progression in prone in an infant aged 8 months. The figure is based on frames from 1 min of video recording. Published with permission of the parents.

1985).

Next, mostly between 6 and 10 months of age, infants develop the ability to crawl on hands and knees with the belly lifted from the support surface (WHO Multicentre Growth Reference Study Group, 2006). Initially, hands and knees are placed in varied patterns. But after about two weeks of experience the most proficient diagonal pattern of limb placement is selected as the preferred pattern (Freedland and Bertenthal, 1994). While the compositional pattern of diagonal gait becomes the dominant pattern, muscle activity in arms and legs is still characterized by varied co-activation of antagonistic muscles. This variation in temporal modulation is larger in the leg muscles than in the arm muscles, presumably because the arms mainly function as relatively simple struts, whereas the legs are especially in charge of varied propulsion (Xiong et al., 2016). With increasing age and growing experience crawling proficiency improves, i.e., the steps become larger and velocity increases (Adolph et al., 1998). Adolph and co-workers also showed that crawling on hands and knees is more efficient in infants who substantially explored belly crawling with many varied postures than in infants who used belly crawling to a limited extent only (Adolph et al., 1998).

Between 10 and 14 months the majority of infants achieves the

ability to walk independently (WHO Multicentre Growth Reference Study Group, 2006). As mentioned previously, learning to walk is initially accompanied by an estimated 100 falls per day (Adolph et al., 2012). Nevertheless, progression by means of early walking is more attractive to infants than progression by means of proficient crawling, as walking has the advantages of being better able to visually explore the environment, and providing more varied opportunities for play and social interaction (Adolph and Tamis-LeMonda, 2014; Dosso and Boudreau, 2014).

Early walking is characterized by variation both in terms of the kinematic parameters of the movements of the leg joints and in terms of EMG parameters (Chang et al. 2006; Polk et al., 2008). The EMG-studies of Lacquaniti and colleagues showed that two additional EMG-patterns are added to those of the neonatal stepping repertoire: one at touch-down of the foot and one at lift-off. The new patterns assist the generation of the shear forces required to decelerate and accelerate the body, respectively (Lacquaniti et al., 2012). With increasing walking experience children increasingly often select preferred muscle activation patterns, e.g., patterns with reciprocal activation of antagonistic leg muscles, out of the varied repertoire of EMG-patterns (Chang et al., 2006). Also the kinematic parameters indicate that increasing

experience is associated with the selection of preferred patterns (Polk et al., 2008). An example is the increased selection of the heel-strike pattern - that characterizes adult gait - from the early repertoire of varied foot placements (Cioni et al., 1993). The processes of adaptive selection are accompanied by improved walking proficiency, i.e., a decrease in step width and increases in step length and walking velocity - changes that occur especially during the first three months of walking experience (Chang et al., 2006; Ledebt et al., 1995; Sutherland et al., 1988).

#### 4.3. Summary of gross motor development

Prenatally the fetus is engaged in varied movements; these mainly consist of GMs, but also include stepping movements. Studies demonstrated that the basic neural organization of postural control and locomotor movements is already functionally active in the first weeks after term: the activity of the CPG-networks of direction-specific postural adjustments and stepping movements is modulated by supraspinal activity, giving rise to varied expression of the CPG-activity. It reflects the phase of primary variability in gross motor development: varied behavior with limited capacities to adapt. For instance, the infant has limited abilities to stabilize the head on the trunk. From 3 to 4 months onwards, the phase of secondary variability develops. The infant learns to stabilize the head on the trunk and learns to propel itself through the environment. Through a process of learning through continuous exploration and trial and error experience, the infant improves its ability to select the best motor strategies from its repertoire. The infant increasingly masters motor abilities requesting upright postures - sitting, standing and walking - with their alleged advantages for visual exploration and social interaction. In addition, the infant increasingly learns to anticipate its postural activity, especially during the first months of upright locomotion.

### 5. Fine motor development

Fine motor function comprises the ability to reach for objects, to lift, carry, and manipulate them. Typically these actions are performed by the upper extremities. They often involve a transport component that moves the hand from the starting position to the object (reaching) and a manipulation component in which the object is grasped (manipulation). In adult persons both components are highly coordinated (Jeannerod, 1998).

#### 5.1. Development of reaching

Ultrasound studies demonstrated the presence of hand-face contact from 10 to 12 weeks PMA and thumb sucking from 15 weeks PMA onwards (De Vries et al., 1985; Hepper, 2013). This may imply that goal directed activity of the upper extremities is already present in the first trimester of gestation and emerges in the absence of visual information. Throughout pregnancy fetal hand motility varies, with about one third to half of the hand movements being directed to mouth, face or head (Sparling et al., 1999). With increasing fetal age the lower and perioral parts of the face are more often touched, at the expense of a decrease of movements directed to the upper parts of the face (Reissland et al., 2014). This redistribution of hand activity is accompanied by a differentiated velocity profile: movements directed to the upper part, or rather to the eye, reach their target with a slower speed than those directed to the mouth region. The latter suggests that movement velocity is adapted to some extent to the delicacy of the target (Zoia et al., 2013).

In the first 2–3 months after term age, babies - like fetuses - direct about one third or half of their hand movements to the face. They do this spontaneously and also when an object is put into their hand (Lew and Butterworth, 1997). From 4 months onwards, they move their hands more frequently to its target location, the mouth, especially when

the hand holds an object. At 5 months this is accompanied by anticipatory opening of the mouth (Lew and Butterworth, 1997). From 2 months onwards, object exploration becomes increasingly multimodal, i.e., the objects are explored both orally and visually. At 2–3 months the exploration usually starts at the mouth, whereas at 4 months visual exploration gets priority (Rochat, 1989). The latter is associated with the emergence of fingering of the object, i.e., scanning of the object's surface with the fingertips (Rochat, 1989). Between 4 and 6 months infants also start to transfer objects from one hand to the other (Greaves et al., 2012; Rochat, 1989)

In contrast to goal-directed activity to parts of the own body, reaching towards an external object requires the infant to locate the object in space and to translate this information into an upper extremity movement towards the object. Generally, but not necessarily, target location is based on visual information. Van der Meer (1997) demonstrated that term newborns in supine are able to control their arm movements to some extent on the basis of visual information: when put in the dark the infants were able to position their hand in the beam of light available. Indeed, already in the first few days or weeks postnatally term infants may produce arm movements in response to an object (Bower et al., 1970; DiFranco et al., 1978; Von Hofsten, 1982), especially when they fixate the object and when they are put in a sitting position with ample neck and trunk support (creating for the infant a state of so-called 'liberated motor activity'; Amiel-Tison and Grenier, 1983). These so-called 'prereaches' may consist of oscillating or flapping movements of the extended arms that generally are not clearly directed to the object, or of movements which bring the hands to the mouth (Van der Fits et al., 1999b). Around the age of 3 months object presentation often elicits 'prereaches' (Trevarthen, 1984; Von Hofsten, 1984). Between 4 and 5 months reaching rapidly becomes successful, i.e., it ends in grasping of the object (Van der Fits et al., 1999b). The developmental sequence of pre-reaching to successful grasping is paralleled and facilitated by the simultaneous improvement of the visual system, including the development of stereopsis. The precursor of stereopsis (binocular summation) emerges at 2 months and stereopsis itself at 4–5 months (Norcia and Gerhard, 2015). The emergence of successful reaching may be enhanced by active trial and error reaching experiences (Libertus and Needham, 2010; Lobo and Galloway, 2008; Lobo et al., 2004; Williams et al., 2015). Libertus and Needham (2010) combined the active practice of reaching experience with the application of 'sticky mittens', i.e., the combination of Velcro mittens and Velcro-covered toys. This also resulted in an accelerated emergence of successful reaching. Most likely this positive effect was mainly - but not exclusively - brought about by the active practice and less by the 'sticky mittens' (Wiesen et al., 2016; Williams et al., 2015).

The first successful reaching movements are characterized by variation: variation in trajectory, in movement velocity, movement amplitude and movement duration (Thelen et al., 1993; Von Hofsten, 1991). The early reaching repertoire contains reaches that are rather straightforwardly directed to the object and a variety of movements that consist of multiple submovements (movement units). Movement units may be determined with the help of the peaks in the velocity profile of the hand (Von Hofsten, 1991). At 4 months reaches consist of 4–7 movement units when performed in supine (De Graaf-Peters et al., 2007; Fallang et al., 2000) and of 3–5 movement units when carried out during semi-reclined sitting or upright supported sitting (median values; De Graaf-Peters et al., 2007; Konczak et al., 1995; Von Hofsten, 1991). The data indicate that for young infants reaching in supine is more challenging than reaching in supported sitting, presumably due to the larger antigravity effort required in the former situation. In the following two months, the number of movement units decreases significantly to 3–4 in supine (De Graaf-Peters et al., 2007; Fallang et al., 2000) and 2.5–3 in supported sitting (median values; De Graaf-Peters et al., 2007; Konczak et al., 1995). The positional advantage of sitting over supine has disappeared (Savelsbergh and Van der Kamp, 1994). Reaching performance between 4 and 6 months also depends on object



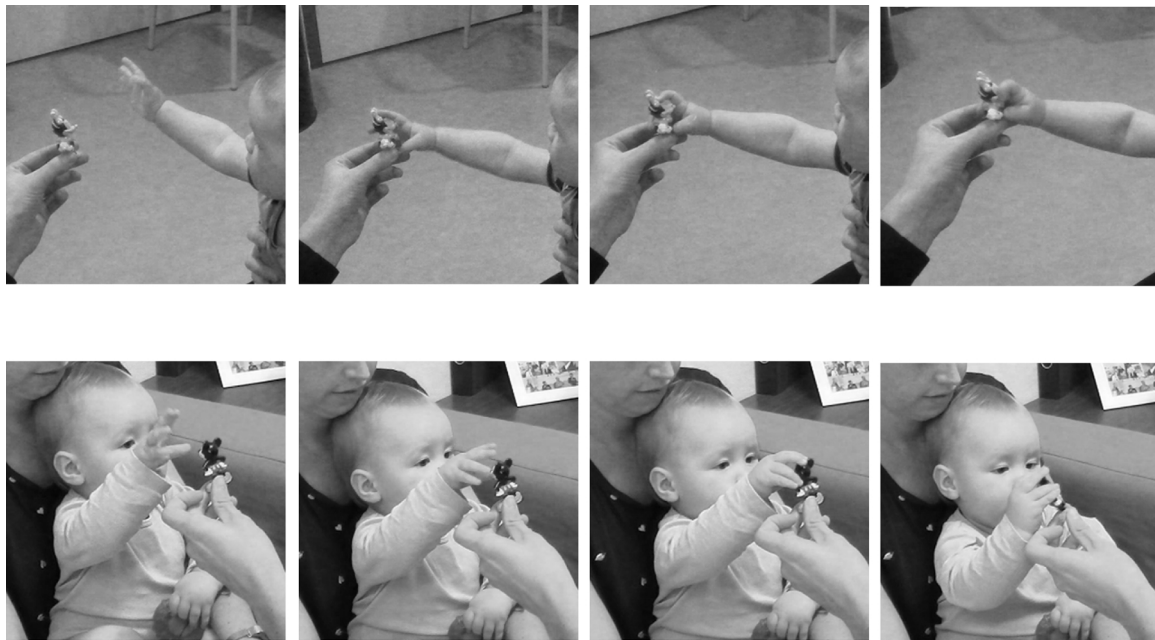


Fig. 5. Two examples of reaching for a toy sampled from video-recordings. Upper panel: a reaching movement of a 6-months-old; the infant does not shape the hand in anticipation to the properties of the object. Lower panel: a reaching movement of a 12-months-old; the infant does adjust hand movements during reaching in anticipation of the object properties. Published with permission of the parents of the infants.

size and rigidity: reaching movements have the least movement units when the object is large and rigid (e.g., a polystyrene ball with a diameter of 12.5 cm), but more when the object is large and soft (a pompom) or small (diameter of 5 cm; Rocha et al., 2013). Initially, infants are also more interested in the larger objects (Libertus et al., 2013).

In the second half year after birth, infants are increasingly more often able to select an efficient, straightforward movement towards the desired object. The number of movement units in sitting position decreases to 2 at the end of the first year (Konczak et al., 1995; Von Hofsten, 1991). This number is larger when the infant reaches in the dark towards a glowing object, suggesting that visual information enhances the selection of an efficient reaching movement (Berthier and Carrico, 2010). The adult level of reaching, characterized by the consistent use of movements preprogrammed with one movement unit, is achieved during sitting with ample postural support at the age of 2 years (Konczak and Dichgans, 1997). However, during sitting without ample support, the adult level is first reached around the age of 7 years (Kuhntz-Buschbeck et al., 1998).

From fetal age onwards arm movements consist of varied bilateral and unilateral movements with a unilateral preference (Corbetta and Thelen, 1996; De Vries et al., 2001; Fagard et al., 2009). From the moment that infants develop goal-directed reaching, they are increasingly able to adjust the unilateral or bilateral nature of their arm movements to the size of the object: at 6 months infants clearly prefer bilateral reaches when presented a relatively large ball (Van Hof et al., 2002). Rochat (1992) demonstrated that also postural support and postural achievement in terms of being able to sit independently affect the nature of infant's reaching movements: non-sitting infants preferred bilateral reaches when placed in supine, semi-reclined sitting or prone-reclined position, but unilateral reaches in supported upright sitting. Yet, infants who could sit without help favored unilateral reaches in all conditions. The dominance of unilateral reaches in the sitting infants may not only be explained by the achievement of the sitting ability, but may also be attributed to general developmental progress associated with increasing age (Sgandurra et al., 2012). Notwithstanding the increase of unilateral reaches with increasing age, 6–12 months old infants show a large variation in arm-hand use during simple grasping

tasks: they prefer right hand grasps (about 50%) to left hand grasps and bimanual grasps (each about 25%; Fagard and Lockman, 2005). Interestingly, some studies reported a temporary re-emergence for preferred bilateral reaching when infants start to cruise (Atun-Einy et al., 2014) or start to walk independently (Corbetta and Bojczyk, 2002). This temporary 'regression' may reflect the sensorimotor recalibration and reorganization of postural abilities occurring in the period that the infant develops standing and walking (Chen et al., 2016).

## 5.2. Development of manipulation

Finger movements are present from 12 weeks PMA (De Vries et al., 1984). Isolated finger movements and sequences of finger movements may be observed during GMs in the preterm and early postnatal months, however fisting is the predominant movement (Ferrari et al., 2016; Wallace and Whishaw, 2003). The isolated finger movements reflect the presence of functional monosynaptic corticospinal connections to the cervical spinal cord, which are present from 24 weeks PMA (Eyre et al., 2000, 2007). Nagy et al. (2005) showed that full-term newborn infants are able to imitate an index finger protrusion movement shown by an adult person, and increasingly better and more often when experience during the test increased. The baby's capacity to imitate finger gestures corroborates the functional activity of the mirror neuron system at term age.

From 3 months post-term, fisting decreases and sequential and isolated finger movements during spontaneous movements increase (Ferrari et al., 2016; Wallace and Whishaw, 2003). During early grasping (4–5 months) mostly the palmar grasp is observed, i.e., the grasp in which the whole palmar surface and all fingers (with or without the little finger) are used (Halverson, 1931; Newell et al., 1989; Touwen, 1976). However, when small objects (1–2 cm) are presented to 4-months-olds they may show a large variation of grips, varying from palmar grasp to movements with only thumb and index finger (Newell et al., 1989). With increasing age, especially after the age of 6 months, the frequency of grasping movements with only thumb and index finger increases (Halverson, 1931; Touwen, 1976). Grasping gets increasingly adapted to the form of the object (Newell et al., 1989). Thumb and index finger movements become more specialized: at 6–9 months the

scissor grasp (with extended thumb and index finger) dominates, at 9–14 months the inferior pincer grasp (with extended thumb and flexed index finger), and from about 14 months the pincer grasp (with flexion of thumb and index finger) is frequently observed (Touwen, 1976).

In the second half year postnatally, infants improve their ability to adapt the configuration and orientation of the hand during reaching with respect to object shape and orientation (Fig. 5; Berthier and Carrico, 2010; Karl and Whishaw, 2014; McCarty et al., 2001; Von Hofsten and Fazel-Zandy, 1984). Their increasing ability to select a well-adapted hand orientation does not depend on the visibility of the hand during grasping, implying that it is largely determined by feed-forward motor control (McCarty et al., 2001). Pre-shaping of the hand to detailed object properties is, however, worse when infants grasp a glowing object in the dark compared to natural light conditions (Berthier and Carrico, 2010). This suggests that visual information on target properties does play a role in the planning of hand movements during reaching.

From 7 months onwards, infants develop role-differentiated bimanual manipulation, implying that each hand performs a different but complementary action to handle an object (Kimmerle et al., 1995). This ability improves with increasing age. However, at the age of 13 months role-specific bimanual actions only form 20% of the infant's play actions with toys promoting such actions (Kimmerle et al., 2010).

At the end of the first year infants also are able to adjust lifting movements to the object's weight on the basis of prior trial and error experience (Mash et al., 2014). Nevertheless, it takes many years before children are able to lift objects in the precisely coordinated and efficient way of adults with its paralleled preprogramming of grip force and load force. One-year-old children generate the grip force and load force sequentially and produce downward directed load forces in the pre-lifting phase (Forssberg et al., 1991). The parallel preprogramming of the forces and the ability to subtly fine-tune the forces to the specifics of the situation gradually improves and reaches its adult form between 8 and 11 year (Forssberg et al., 1992). The development of the coordination of forces during object lifting illustrates the protracted developmental course of manual skills in general. For instance, the ability to perform a peg-board task or a rapid tapping task increases substantially between 2 and 13 years (Müller and Hömberg, 1992). The developmental changes in precision and complex manipulations are paralleled by a pronounced decrease in corticomotoneuronal delay. This suggests a contribution of the developmental changes in the corticospinal tract to the development of the manual skills (Eyre, 2007; Müller and Hömberg, 1992).

The use of arm and hands is intimately interwoven with the infant's capacities to control posture and its position (Hadders-Algra, 2013; Thelen and Spencer, 1998). For instance, De Graaf-Peters et al. (2007) demonstrated in 4–6 months old infants a positive association between direction-specific postural adjustments and success and kinematic quality of reaching. We noted in the previous section, that supported sitting in young infants is associated with more success of reaching than the supine position. Supported sitting also results in more visual exploration of toys, whereas supine is associated with more oral exploration (Soska and Adolph, 2014). Yet, in both positions infants' most frequent activity with a toy is fingering and object rotation (Soska and Adolph, 2014). In the phase that infants learn to sit without support, hand use during independent sitting varies between offering postural support and reaching activities with both arms. When sitting skills improve and infants master weight shifting, they become increasingly successful in using their arms for reaching activities (Harbourne et al., 2013).

### 5.3. Summary of fine motor development

Young fetuses exhibit goal directed arm and hand movements, especially to their face. This prenatal activity and its associated haptic

and proprioceptive information result in arm movements that already can be adapted to some extent to the nature of the facial target. After birth, the situation changes, also visual information has to be integrated. Notwithstanding the fact that neonates can adjust arm movements to a limited extent on the basis of visual information, the presence of visual information induces a phase of recalibration in the upper extremity movements (Zoia et al., 2013). The ability to use and integrate visual information for reaching and grasping improves drastically at 3–4 months, an improvement that is largely facilitated by the developmental progression of the visual system and the ability to stabilize the head – with the visual system – on the trunk. In the second half of the first post-term year secondary variability emerges: the infants gradually learn to adapt the arm and hand movements to the constraints of the situation. It takes many years before the secondary phase has reached its adult configuration. This is especially true for the manipulative abilities, most likely due to the protracted developmental changes occurring in corticospinal activity.

## 6. Oral motor development

Oral motor behavior basically serves two functions: the ingestion of food by means of sucking, biting, chewing and swallowing, and communication by means of vocalizations or spoken words.

### 6.1. Development of oral motor behavior involved in food intake

For many years, infant oral motor behavior had been described in term of reflexes and responses, e.g., the rooting reflex (head turn in the direction of the stimulated perioral skin accompanied by mouth opening and 'labial grasping') and the sucking response (rhythmical sucking induced by the insertion of a nipple or finger into the infant's mouth; Precht, 1977; Sheppard and Mysak, 1984). Gradually it became clear, however, that most oral motor behavior, especially sucking, chewing and swallowing, is organized with the help of CPG-networks located in the brainstem. These networks are modulated by supraspinal activity and exhibit experience-dependent plasticity (Barlow, 2009; Delaney and Arvedson, 2008).

Fetal sucking and swallowing movements have been observed from 12 weeks PMA onwards; they may include thumb sucking (De Vries et al., 1982). Sucking movements emerge at the same age as the rooting reflex. The latter was reported by Minkowski (1938), who studied motor behavior of fetuses in a bath of physiological saline, immediately after they had been delivered to safe maternal life. The incidence of sucking and swallowing movements in the first half of gestation is low (De Vries et al., 1985). Moreover, the first jaw, lip, tongue and pharynx movements are relatively simple (Miller et al., 2003). The movements become gradually more complex: simple jaw and lip opening movements develop into repetitive mouth opening and closing movements similar to those present in neonatal sucking, and tongue movements develop from simple forward thrusts and cupping movements to the anterior-posterior movements needed for the successful sucking of the neonate. The latter behavior is consistently present from 28 weeks PMA onwards and is used during fetal sucking and swallowing. Fetal sucking and swallowing is clearly associated with hand-face contact (Miller et al., 2003).

After birth, nutritive sucking and swallowing have to be combined with respiration. This is a challenging task, which is not well mastered at 32–33 weeks PMA. At that age sucking, swallowing and respiration is characterized by exploration of the possible combinations to coordinate the three activities. The infants do not only show the swallow-expiration sequences that are typical for later life (Kelly et al., 2007), they also exhibit, for instance, breathing during swallowing, and alternating blocks of suck-swallow (without respiration, lasting 5–7 seconds) and respiration (without swallowing, lasting 10–16 s; Vice and Gewolb,

2008). From about 34 weeks PMA, total oral feeding may be achieved in low risk infants (Delaney and Arvedson, 2008). At that age and in the few following weeks, sucking and swallowing is characterized by a large variation in tongue movements, and by a suck-swallow ratio that is higher than the typical 1:1 ratio of the full-term newborn (Bullock et al., 1990). With increasing age, in particular after 36 weeks PMA, the frequency of typical and efficient tongue movements increases, the sucking rhythm stabilizes with a dominant 1:1 suck-swallow ratio, and sucking is less often interrupted by breathing bursts (Bullock et al., 1990; Gewolb et al., 2001; Gewolb and Vice, 2006; Vice and Gewolb, 2008). The phase of secondary variability emerges.

Craig and Lee (1999) demonstrated that the sucking of term newborns is characterized by well adapted pressure changes, that have kinematic characteristics similar to those exhibited during adult sucking. This finding supports the idea that term newborns are with sucking behavior in the phase of secondary variability. Like the preterm infants, also term born neonates face the challenge to combine sucking and swallowing with respiration. During the first postnatal days the infants explore various combinations, be it without breathing during swallowing, and the alternating blocks of suck-swallow and respiration shown at early preterm age (Bamford et al., 1992; Kelly et al., 2007; Weber et al., 1986). At this early age about half of the swallows occur mid-expiratory (Kelly et al., 2007). However, already at one week postnatally this pattern ceases to be the most prevalent one; the adult timing of swallowing emerges, i.e., swallowing at the cusp of inspiration and expiration. This coordination pattern occurs at the age of one week in 30% of swallows; its prevalence increases with increasing age to 37% at 6 months, and 75% at 12 months (Kelly et al., 2007). During the first postnatal months, sucking efficiency increases: the number of sucks per minute increases, the length of sucking bursts increases, and more milk per unit time is transferred (Qureshi et al., 2002; Sakalidis et al., 2013). The latter is associated with a doubling of milk intake in the first postnatal month (volume of milk per suck; Qureshi et al., 2002).

During the first post-term months infants are fed human milk or infant formula. From the age of 4 to 6 months also other types of food are introduced, delivered on a spoon instead of by breast or bottle (Wilson et al., 2012). The infants initially get semisolid foods, e.g., pureed food, which is orally explored and handled by sucking and munching (Gisel, 1991). Soon thereafter, usually from 6 months onwards, infants can also handle solid food; the chewing movements emerge. At 7 months of age, the chewing rate and the number of chewing cycles are already adapted to the texture of the food (puree, semisolid, solid; Wilson et al., 2012). The chewing rate does not change with increasing age, but chewing efficiency improves between 6 and 24 months: less chewing cycles and less time is needed to grind food (Gisel, 1991). This is accompanied by an increasingly better lip control, increased efficiency of tongue movements, and a decreased involvement of the perioral structures in the act of swallowing (Stolovitz and Gisel, 1991). Steeve et al. (2008) showed that at 9 months the coordination of the activity of the masseter and temporal muscles (bilaterally) and their antagonist, the anterior belly of the digastric muscle, was characterized by the basic coordination of adults, but expressed with large variation in the exact timing and degree of contraction of the muscles. With increasing age – at least until the age of 4 years – the synchrony of agonistic activity and reciprocal antagonistic activity increases (Green et al., 1997; Steeve et al., 2008), suggesting a better selection of the adult pattern of efficient muscle coordination (Fig. 6).

## 6.2. Development of oral motor behavior involved in communication

During the second half of gestation facial movements, such as the inner brow raise or lip parting, become increasingly more organized into complex Gestalt movements, e.g., the ‘cry-face Gestalt’, the

‘laughter-face Gestalt’ and the ‘pain/distress-face Gestalt’ (Reissland et al., 2011, 2013). After birth, facial motility produced in the absence of communication and feeding is characterized by large variation including cry- and smile Gestalts (Green and Wilson, 2006). Between 5 and 10 weeks post-term the infant learns to select the smiling expression in response to another human’s face: social smiling emerges (Touwen, 1976). During the first postnatal year, non-communicative facial movements increase in number and speed, the epochs with these movements decrease, and the coupling between the various facial movements increases. The latter is especially true for the lower lip and jaw at the end of the first year. This may be regarded as an assist to speech development (Green and Wilson, 2006).

Since the first publication on neonatal imitation of facial movements by Meltzoff and Moore (1977), this issue has been vigorously debated. It is clear that human newborns have a specific interest in human faces (Johnson et al., 2015). Reid et al. (2017) were even able to demonstrate that also fetuses of 33–36 weeks PMA have a preference for face-like stimuli. However, increasing evidence suggests that the young infant’s ability to imitate facial movements of an adult person is limited to tongue protrusion movements (Johnson et al., 2015; Jones, 2017; Meltzoff et al. 2017).

Speech development heavily relies on the presence of sensory information. In typically developing infants the information predominantly consists of auditory information, which is enhanced by concomitant visual information (Kuhl and Meltzoff, 1982); infants with hearing impairment especially rely on visual information. Term fetuses and term neonates already exhibit a preference for the voice of their mother, which they can distinguish from the voice of a female stranger (DeCasper and Fifer, 1980; Kisilevsky et al., 2003). Newborns also can distinguish between native and non-native vowels, e.g., the English /i/ versus the Swedish /y/ (Moon et al., 2013). These data suggest that the complex processes of language learning already start in the prenatal period. Before the age of 8 months infants are able to distinguish many of the 800 worldwide available phonemes (the basic sounds of a language; each language has a unique set of about forty phonemes; Kuhl, 2010). However, before the first words emerge, so-called perceptual attunement occurs, i.e., at 10–12 months infants are no longer able to discriminate non-native consonants that are absent in their own language. For instance, 8-months-old Japanese babies are able to distinguish the /r/ and the /l/ - consonants that are pronounced similarly in the Japanese language - but they have lost this ability at 10–12 months; the perception of these consonants has disappeared from their repertoire (Kuhl, 2010; Werker and Hensch, 2015). Interestingly, a similar process of perceptual narrowing occurs in face recognition. Infants aged 6 months recognize both human and monkey faces, but at the age of 9 months recognition is restricted to human faces (Pascalis and Kelly, 2009).

From early postnatal age onwards, infants do not only produce non-speech utterances, such as crying, laughing and ‘vegetative’ sounds, but also so-called protophones, i.e., precursors of speech. Protophones may be flexibly associated with different affects (positive, negative, neutral), which turns them different from the more stereotyped utterances, such as crying and laughing, that are strictly linked to one affect (Jhang and Oller, 2017). With increasing age, the repertoire of protophones gradually expands, and the protophones themselves become increasingly complex (Nathani et al., 2006). Between 3 and 5 months, infants increasingly often select from the varied infant vowel repertoire the vowels that have adult-like frequency characteristics. Most likely, this vowel selection is enhanced by imitation of adult speech (Kuhl and Meltzoff, 1996). In this respect it is interesting to note, that especially at early age, human faces constitute a substantial proportion of the visual scenes of an infant’s waking hours (Jayaraman et al., 2015), thereby offering ample opportunity for communicative interaction.

Between 5 and 10 months of age canonical (or reduplicated)



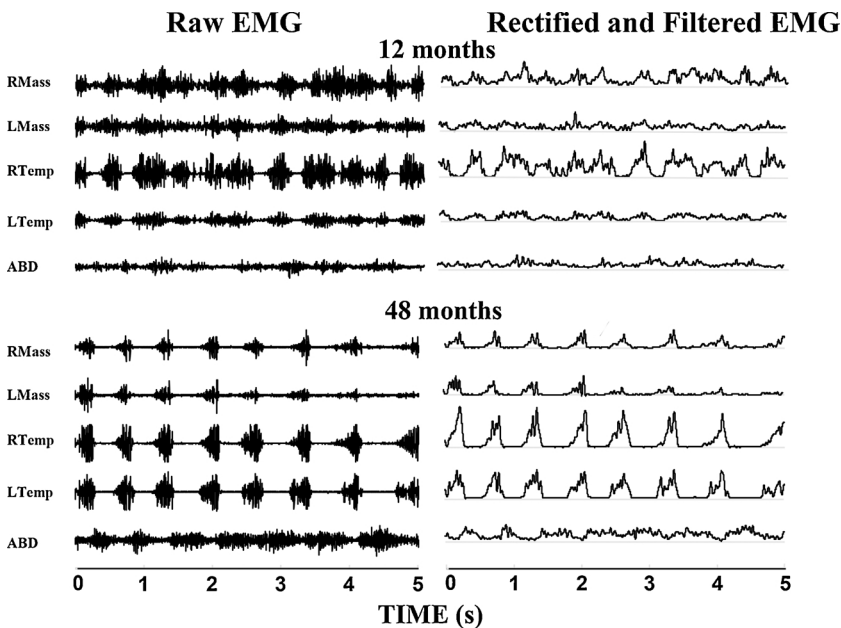


Fig. 6. EMG-activity during chewing of the same child at 12 months and 48 months. The left panels show the raw EMG-activity, the right panels the rectified and filtered panels. The figures illustrate that a) the basic adult pattern of coordination is already present at 12 months, and b) that the variation in EMG-activity is considerably larger at 12 months than at 48 months. RMas = right masseter, LMas = left masseter, RTemp = right temporalis, LTemp = left temporalis, ABD = anterior belly of digastric. Adapted from Green et al. 1997, with permission.

babbling develops (e.g., /dada/ or /mama/), and a bit later and temporally largely overlapping with the former, variegated babbling (e.g., /kadabyda/; Stark et al., 1993; Nathani et al., 2006). From about 12 months the first words emerge; the acquisition of the first words is a slow process, but from 18 months onwards vocabulary development dramatically accelerates (Kuhl, 2010). Studies on oral motor coordination (Moore and Ruark, 1996; Steeve et al., 2008) showed that speech at 12 months is associated with a pronounced jaw displacement, accompanied by excessive compression of the lips during oral closure, and a large variation in lip movements. At 2 years, the lip movements become relatively larger and the jaw movements smaller. The lip movements are highly synchronized. This synchronization, which differs from the adult lip coordination, may be viewed as a strategy to simplify the motor action. It disappears at preschool age (Moore and Ruark, 1996; Steeve et al., 2008).

### 6.3. Summary of oral motor development

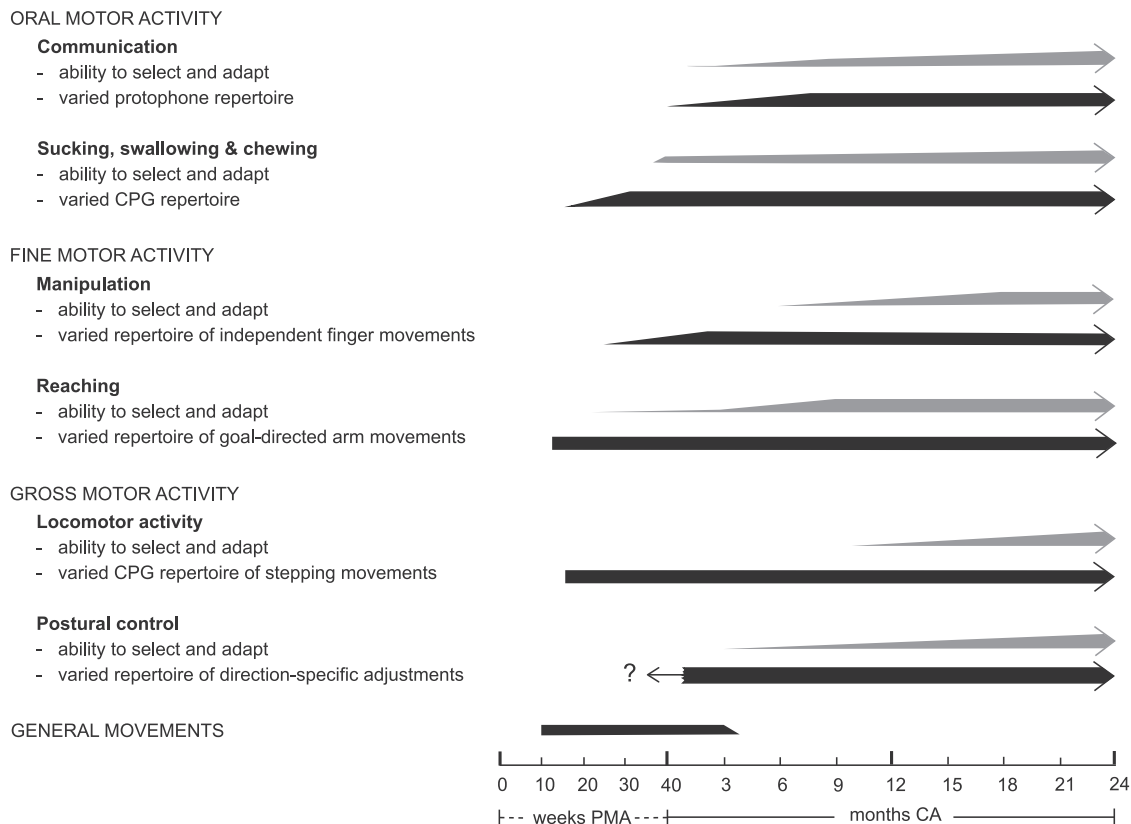
Sucking and swallowing are already present at early fetal age. Prenatal development and experience results in adaptive sucking and swallowing from 36 weeks PMA onwards: the phase of secondary variability starts. The secondary variability also allows for an adequate integration of feeding and respiration, as soon as the term infant is born. Chewing emerges from 4 months onwards, first without adaptation, but from 6 months with an increasing ability to adjust the movements to the texture and size of the food. Chewing becomes increasingly efficient, a process that continues at least until preschool age.

From early postnatal age, the infant explores its repertoire of vocalizations. Increasingly often, the infant selects from the vocal repertoire sounds of the native language. In the second half year post-term infants start to produce native strings of vowels and consonants, a development that is paralleled by a perceptual narrowing of sounds that gives priority to native language sounds. Around the age of one year, this results in the production of the first words. Thereafter speech and language development continue for many years. It involves an increase in vocabulary, the acquisition of grammar rules (Parish-Morris et al., 2014), and a better coordination of speech movements. The latter turns speech production increasingly adaptive and efficient, and provides it with increasing possibilities to vary.

### 7. Concluding remarks

Spontaneous activity is a quintessential feature of the nervous system. Already at early fetal age motor behavior is organized by means of activity of basic networks in the brainstem and spinal cord that is modulated by supraspinal activity: the phase of primary variability starts (Fig. 7). The supraspinal activity, first brought about by the cortical subplate and later by the cortical plate, induces movement variation (Hadders-Algra, 2018). In this initial phase of development, the phase of primary variability, movement variation especially serves exploration; its associated afferent information is primarily used to sculpt the developing nervous system, and less to adapt motor behavior to the specifics of the environment. The phase of secondary variability, in which movement variation starts to serve adaptation, begins at function-specific ages (Fig. 7). In sucking and swallowing - functions with a high survival value - secondary variability emerges shortly before term age. In gross and fine motor development, and in oral motor behavior involved in chewing and speech, it emerges from 3 to 4 months post-term onwards, i.e., from the time that the cortical subplate has disappeared in the primary sensory and motor cortices and development focuses on the permanent cortical circuitries (Kostović et al., 2014, 2015). With increasing age, and increasing emergence of the permanent circuitries in the frontal, parietal and temporal association cortices, the infants abilities to vary improve. The infant continues to explore by means of trial and error. The experience and its accompanying developmental processes allow the infant increasingly better to use in an adaptive and efficient way upright motor behaviors, manual activities and vocalizations belonging to the native language. As a result, most typically developing infants have achieved by the age of 12 to 18 months the milestones of independent walking, the use of the pincer grasp, and the first words. It takes, however, many years of additional exploration, experience and developmental changes in the brain, before the adult configuration of secondary variability with its efficient adaptability and its freedom to vary is achieved.

Currently we know little about the exact nature of the supraspinal network correlates underlying the transitions from primary to secondary variability. Future studies may address this issue with approaches in which various assessment techniques are combined, e.g., detailed observation of infant motor behaviour, EMG- and kinematic recordings, and multichannel EEG-recordings or resting state functional magnetic resonance imaging – preferably in a longitudinal design.



**Fig. 7.** Overview of the development of the phases of primary and secondary variability in gross, fine and oral motor development. The bottom line denotes age, first in weeks PMA, after term (40 weeks) in months corrected age (CA). The black timelines reflect the development of the varied repertoire, the grey timelines that of the ability to select and adapt. The diagram indicates that the primary repertoires primarily develop prior to term age, whereas secondary variability, i.e., the ability to select and adapt, mainly develops after 3 months post-term. An exception to this rule is the development of adaptive sucking which is present from 36 weeks PMA onwards.

## Declaration of interest

None

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