Neural development and sensorimotor control

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Abstract

What is the relationship between development of the nervous system and the emergence of voluntary motor behavior? This is the central question of the naturenurture discussion that has intrigued child psychologists and pediatric neurologists for decades. This paper attempts to revisit this issue. Recent empirical evidence on how infants acquire multi-joint coordination and how children learn to adapt to novel force environments will be discussed with reference to the underlying development of the nervous system. The claim will be made that the developing human nervous system by no means constitutes an ideal controller. However, its redundancy, its ability to integrate multi-modal sensory information and motor commands and its facility of time-critical neural plasticity are features that may prove to be useful for the design of adaptive robots.

1. Development of coordination

At birth, a human infant can neither reach or grasp. From a control point of view, the completion of two processes are required to perform successful reaching. First, any neural controller must be capable to interact with its "plant" (i.e., the arm in this example) in such a way that centrally planned, complex actions can be executed. Second, visually specified goals must be linked to appropriate motor acts. These motor acts, in turn, must be suitable to move the arm to the desired goal. There are a number of reasons that seem to explain why newborn infants are not equipped to solve these two tasks:

• They have limited postural control of the trunk, head and arms. Appropriate head and trunk righting reactions begin to emerge 2-3 month after birth (Milani-Comparetti and Gidoni 1967).

• They have limited knowledge about the physical makeup of their bodies (i.e. moments of inertia, viscosity, stiffness of their arm segments).

• They have only a limited movement repertoire consisting of an array of infant reflexes (i.e., grasping, sucking), and basal intra- and interlimb synergies (coupled flexor, extensor activity, coactivation) (Bekoff et al. 1989; Hadders-Algra et al. 1992).

• They have limited visual capabilities. During the 1st postnatal month, the visual system provides the infant with functionally useful, but unrefined vision at a level of approximate 5% of adult acuity level. The infant can likely differentiate facial features from a distance of about 50 cm. Objects beyond this distance are probably not seen clearly (Atkinson and Braddick 1981).

• They have not established a finite neural control structure. Most cortico-spinal projections are not differentiated. In a first stage, cortical neurons from all areas of the neocortex send collaterals to subcortical structures - a process termed arborization. In a second stage, these collaterals are pruned according to their later function (e.g., a visual projection, or motor projection - for a review: O'Leary 1992).

Despite all these limitations, babies as early as one week of age will attempt small arm movements directed towards the target, and are capable of orienting towards and tracking a moving object with coordinated rotations of head and eyes, although their heads may wobble considerably (Trevarthen 1980). These early arm movements occur unpredictable, but they are not the result of random activity or pure reflex actions.

A few days after birth infants are also able to perform anticipatory arm movements when trying to intercept a moving target. Von Hofsten (1980) believes that such interceptive actions are triggered by the presence of an object in the field of view. While the arm movements of newborns are characterized by a rather fluid interjoint pattern, reach and grasp motions of two- and three-month old infants reveal either short swiping motions or relatively long lasting jerky movements. These movements appear to be pre-programmed, "ballistic" motions, because trajectory correction is absent (Bower et al. 1970).

About 3 months after the onset of reaching, infants reach consistently for objects in their surround and rarely miss their target. By the same time infants reveal improvements in their manipulative skills (e.g., precision grip). Next to these advancements in the approach phase of the reach, infant motor systems continue to refine the transport phase. Kinematically, their hand paths become straighter, but more important, they now show signs of external force exploitation. For example, they learn that gravity and motion-dependent forces alone can extend their forearms. Consequently, they do not have to initiate elbow extension through muscular activation, but let gravity do the work (Konczak et al. 1997). As a consequence of this learning process, infant movements become more economical - muscles will only be activated when needed. However, an adult-like skill economy will not develop before 24-36 months of age (Konczak and Dichgans 1997).

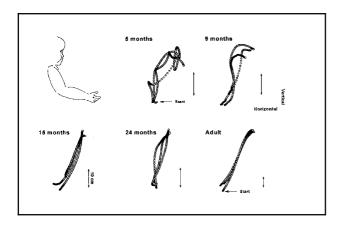


Figure 1: The emergence of goal-directed reaching behavior. Hand paths belong to one infant at four different developmental times. Adult paths for comparison. From: Konczak & Dichgans (1997)

2. Adaptive learning of dynamics

After the onset of reaching, infants begin to manipulate objects that have quite different inertial properties. Thus, it is evident that their motor systems have the ability to adjust their motor output to changes in external forces. When adult humans perform goal-directed arm movements under the influence of an unknown external force, they learn to adapt to these external dynamics. After removal of such an external force field, they reveal kinematic after-effects that are indicative of a neural controller that still compensates the no longer existing force. Such behavior suggests that the adult human nervous system uses a neural representation of the inverse arm dynamics to control upper extremity motion. Central to the notion of an inverse dynamics model (IDM) is that learning generalizes to untrained portions of the workspace. Children as young as 6 years reveal such generalized adaptive learning. Learning to compensate an external damping during force elbow flexion movements transferred to the opposite hemi-field, which indicates that a model of the limb dynamics rather than an association of visited space and experienced force was acquired (Jansen-Osmann et al. 2002). Interestingly, the aftereffects were usually more pronounced in the younger children (6 yrs. vs. 10 yrs. of age), indicating that their estimations of the new force field were biased. The children also took longer to re-adapt to a normal force field, which implies that the neural representations of their actual arm dynamics in middle childhood are still not as solidified as in adults. That is, even at an age, where children routinely and successfully engage in goal-directed activities, the development of their motor control systems is not completed - the neural representations of limb dynamics still lack precision and stability.

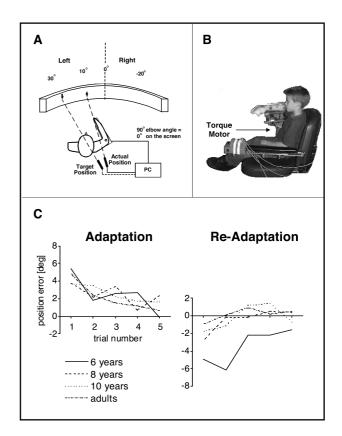


Figure 2: Development of force adaptation. **A.** Subjects performed goal-directed forearm movements against an assisting viscous force. **B.** The viscous force was provided by a computer-controlled torque motor. **C.** Adaptation rates were similar in all age groups, but readaptation was less complete in the 6-year-old children. Shown is here the positional error at the end of the first movement unit. Modified from: Jansen-Osmann et al. (2002)

3. Neural development and behavior

It is widely established that the emergence of voluntary motor behavior does not simply constitute the unfolding of a neural plan, but that orderly neural development is also dependent on the organism's interaction with the environment. The dependency of sensory inputs for the establishment of a functional neuronal circuitry varies between species. Lower organisms and animals with a simple motor repertoire (e.g., gait of horses) often reveal adult-like motor patterns soon after birth. In contrast, non-human primates and humans require sensory stimulation to trigger processes of neural development that will then affect the development of motor control. In addition, the plasticity of the nervous system as well as the development of efferent and afferent projections is timecritical. That is, the organism undergoes "critical" periods of development, where the nervous system expects certain sensory inputs. The deprivation of such stimuli prior to a critical period might have little or no detrimental effects on certain aspects of sensorimotor development, but the failure of such stimulation during such period will negatively affect later sensorimotor function. For example, rearing a monkey for its first three postnatal months under far red illumination to make color vision impossible does not result in long lasting deficits in color vision (Brenner et al. 1990). Or, Hopi Indian infants, whose mobility is restricted in the first few months through the use of cradle boards (Dennis & Dennis 1940) do not show a delayed onset of walking (Harriman & Lukosius 1982).

In contrast, it is known that monocular deprivation of kittens during the second postnatal month leads to a striking change in the physiological organization of the visual cortex such that few cortical neurons remains responsive to the stimulation of the deprived eye (Berardi et al. 2003, Hubel & Wiesel 1964). Moreover, peripheral sensory deprivation also has a negative impact on the development of the motorneurons in mammals (McLennan & Hendry 1981), that is, the paucity of sensory signals has a direct impact on voluntary motor control. The behavioral manifestations are seen in northern Chines babies, who are reared in sand bags (for sanitary purposes), which leads to a restriction of infant's motility. If this practice is continued beyond the first year of life, the child will not only show a delayed motor development, but it will critically impair later motor and cognitive function (Mei 1994).

4. Summary

I have briefly outlined three areas of research that address the issue of how a complex system like a human child acquires motor skills, how skill learning requires adaptive force control and how neural development driven by endogenous and exogenous factors facilitates the emergence of voluntary motor control. Although the notion of *brain plasticity* is likely not easily implemented in an artificial system, an understanding of the neural mechanisms underlying adaptive learning and control in human infants may provide fruitful ideas for the design of adaptive robots.

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