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An action perspective on motor development

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Motor development has all too often been considered as a set of milestones with little significance for the psychology of the child. Nothing could be more wrong. From an action perspective, motor development is at the heart of development and reflects all its different aspects, including perception, planning and motivation. Recent converging evidence demonstrates that, from birth onwards, children are agents who act on the world. Even in the newborn child, their movements are never just reflexes. On the contrary, they are purposeful goal-directed actions that foresee events in the world. Thus, motor development is not just a question of gaining control over muscles; equally important are questions such as why a particular movement is made, how the movements are planned, and how they anticipate what is going to happen next.

Converging evidence from many different fields of research suggests that human movements are organized as actions and not reactions [1], that is, they are initiated by a motivated subject, defined by a goal, and guided by information. Even choice-reaction tasks [2] and sensorimotor synchronization tasks [3] seem to be most appropriately understood in action terms. A reach, for instance, can be executed in an infinite number of ways. It is still defined as the same action, however, if the goal remains the same. Thus, the goal state is already represented when actions are planned [4]. When executing actions or observing someone else performing them, subjects fixate goals and sub-goals of the movements [5]. However, this is only done if an action is implied: when showing the same movements without the context of an agent, subjects fixated the motion instead of the goals [6]. Other recent motor control studies also demonstrate the close relationship between perception and action [7,8].

Evidence from neuroscience shows that the brain represents movements in terms of actions even at the level of neural processes. A specific set of neurons, ‘mirror neurons’, are activated when perceiving as well as when performing an action [9,10]. These neurons are specific to the goal of actions and not to the mechanics of executing them [11]. Another remarkable example of this type of representation is the finding that corresponding brain areas are activated in the production of spoken language in hearing subjects and sign language in deaf subject [12].

Infants’ perception and planning of movements seem to follow similar principles as those for adults. When reaching for an object the posture of the hand will adjust to the size and orientation of the object before or during the approach to it [13,14]. Claxton *et al.* [15] found that 10-month-old infants picked up a ball differently, depending on whether the intention was throw it into a tub or to fit it into a tube. Infants imitate the purpose of actions rather than their exact form [16] and the tendency to imitate actions depends on how interesting their effects or outcomes are [17,18]. Also when observing actions performed by others, infants attend to the purpose of the movements rather than their exact form [19–21]. Thus, it seems that adults and infants alike perceive and plan movements in terms of actions.

An action approach to motor development has several important implications. First, it gives central importance to the planning and prediction of movements. Actions are directed to the future and must predict what is going to happen next. Such prospective control is based on knowledge about rules and regularities that govern events in the world and abilities to extract future-oriented information from the senses. Second, an action approach stresses motivational factors in motor development. What are the factors that make children want to explore and learn about significant objects and events in the world, and what are the factors that make them explore and learn to control their own movements? Finally, an action approach stresses perceptual guidance of movements rather than the acquisition of motor programs. How do perception and action become integrated in ever more flexible means of attaining desired goals?

Neonatal actions

Actions are fundamentally different from reflexes. According to Sherrington, a reflex is a hardwired sensorimotor loop organized at a spinal or para-spinal level. Reflexes are not goal-directed or driven by motivation. Although reflexes can serve important functions for the subject, they are stereotyped, elicited, and automatic. The movements of newborn infants have traditionally been described as reflexes. Converging evidence, however, shows that most neonatal behaviours are prospective and flexible goal-directed actions. This should not be surprising. Sophisticated pre-structuring of actions at birth is the rule rather than the exception in mammals. When neonatal reflexes are re-examined they often turn out to be goal-directed actions. Rooting, the fact that when

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the skin in the lower part of the face is touched, the infant moves the mouth there, is such a case [22]. This movement is not automatic. If the infant touches him or herself, or is just not hungry, no rooting is initiated. Neither is sucking a reflex. The best evidence for this comes from Craig and Lee, who showed that neonatal sucking relies on prospective monitoring of the flow of milk [23]. Neonates will alter their sucking in preference to their mother's voice over another voice [24]. Furthermore, neonates control their gaze and direct it to significant sources of information like contours, corners [25], faces and eyes [26]. Neonates imitate facial gestures just minutes after birth and the imitation is by no means automatic [27].

A sensorimotor link between eye and hand is already established in the neonate. Von Hofsten found that the newborn infants aimed their extended arm movements towards an object when fixating it [28]. Other evidence suggests that newborn infants make an effort to view their hands. Van der Meer *et al.* placed neonates on their back with the head turned to one side [29]. In this posture neonates tend to extend the arm on the side where the head is turned (the ipsilateral arm) and flex the other one (the contralateral arm). This posture is generally assumed to be a reflex (the Asymmetric Tonic Neck Reflex, ATNR). Is this a reflex or do the neonates extend their arm in order to be able to see it? When both arms were gently pulled downwards, it was found, in accordance with the reflex assumption, that the ipsilateral arm resisted this pull. However, when both arms were occluded from view neither arm resisted the pull. When a TV monitor showing the contralateral arm was placed between the infant and the ipsilateral arm, the infant resisted the pull of the contralateral arm (see Figure 1). This demonstrates that the infant is in control of the arm movements in the ATNR.

In another experiment, van der Meer placed a narrow beam of light in front of the infant, the surroundings otherwise being dark [30]. She measured spontaneous arm-waving movements while the infant lay supine, and found that the neonates put their hands within the light beam where they could see them. They controlled the position, velocity and deceleration of their arms so as to keep the hand visible in the light. When the position of the beam was altered, the hand moved to the new position of the beam. The function of these kinds of basic skills, I suggest, is to provide activity-dependent input to specific sensorimotor systems. By closing the visual–manual loop the infant can begin to explore the relationship between commands and movements, between vision and proprioception, and discover the possibilities and constraints of manual movements.

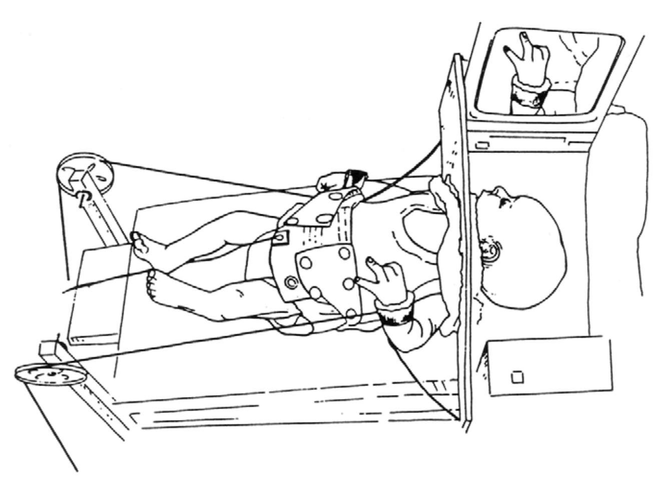

Figure 1. In the experiment of van der Meer *et al.* [29], a newborn infant can see its left hand on the TV monitor while turning its head to the right. The strings on the wrist are attached to small weights pulling them downwards. In this situation, the infant resists the pull of the contralateral arm by the weights, showing that the infant is in control of her arm movements. Reproduced with permission from [71].

The development of action

Action systems do not appear ready-made. Neither are they primarily determined by experience. They are the result of a process with two foci, one in the central nervous system and one in the subject's dynamic interactions with the environment. The brain undoubtedly has its own dynamics that makes neurons proliferate, migrate and differentiate in certain ways and at certain times. However, the emerging action capabilities are also crucially shaped by the subject's interactions with the environment. Without such interaction there would be no functional brain. Perception, cognition and motivation develop at the interface between neural processes and actions. They are a function of both these things and arise from the dynamic interaction between the brain, the body and the outside world. A further important developmental factor is the biomechanics of the body: perception, cognition and motivation are all embodied and subject to biomechanical constraints. Those constraints change dramatically with age, and both affect and are affected by the developing brain and by the way actions are performed.

The nervous system develops in a most dramatic way over the first few months of postnatal life. During this period, there is a massive increase in the connectivity of the cerebral cortex and the cerebellum [31,32]. Once a critical mass of connections is established, a self-organizing process begins that results in new forms of perception, action and cognition. The emergence of new forms of action always relies on multiple developments [33]. The onset of functional reaching depends, for instance, on differentiated control of the arm and hand, the emergence of improved postural control, precise perception of depth through binocular disparity, perception of motion, control of smooth eye tracking, the development of muscles strong enough to control reaching movements, and a motivation to reach.

In summary, the development of action and perception, and the development of the nervous system and growth of the body mutually influence each other in the process of forming increasingly sophisticated means of solving action problems. With development, the different action systems also become increasingly future-oriented and integrated with each other. Ultimately every action engages multiple coordinated action systems.

The importance of motivation

Internally generated motives are crucial for the formation of new behaviour and the maintenance of established behaviour patterns [34]. For example, before infants master reaching, they spend hours and hours trying to get the hand to an object in spite of the fact that they will fail, at least to begin with. For the same reason, children abandon established patterns of behaviour in favour of new ones. For instance, infants often try to walk at an age when they can locomote much more efficiently by crawling. In these examples there is no external reward. It is as if the infants knew that sometime in the future they would be much better off if they could master the new activities. The direct motives are, of course, different. I have argued earlier that children find pleasure in exploring their action possibilities [35]. When new possibilities open up as a result of, for example, the establishment of new neuronal pathways, improved perception, or biomechanical changes, children are eager to explore them. At the same time, they are eager to explore what the objects and events in their surrounding afford in terms of their new modes of action [36].

The development of prospective control

Anticipating one's own actions

If mastery of actions relies on the perception and knowledge of upcoming events, then the development of actions has to do with acquiring systems for handling such information. It has to do with anticipating both one's own posture and movements, and future events in the world. For every mode of action that develops, new prospective problems of movement construction arise and it takes time to acquire ways to solve them. At the onset of functional reaching, infants approach the goal in a series of sub-movements [37,38]. A few months later, the movement has become smooth and organized into a smooth approach and one grasping movement.

One of the most challenging problems infants encounter is to control posture. Because of its central role in movement production, postural control becomes a limiting factor in motor development. All actions produce inertial forces and displace the point of gravity of the body. To maintain balance these forces have to be negotiated ahead of time. We have found that such prospective control develops in parallel with the mastery of postural control [39,40] (see Box 1).

Predicting external events

Smooth-pursuit eye movement is the earliest action that predicts external events. Before it appears, visual tracking is primarily saccadic and geared to object position. The emergence of smooth pursuit is extremely rapid [41–43] (Box 2), and shows a distinct pattern of development. When it first appears, it is well timed to the external motion but the gain is low and the pursuit is supplemented by saccades. Its development follows closely the improvements in sensitivity to visual motion direction [44]. In sharp contrast to the rapid development of smooth pursuit, the head movements that generally accompany visual tracking lag profoundly even months after smooth pursuit has been established [41]. This suggests that prospective control is not a general ability but specific to each mode of action. It is important to note that predictive gaze tracking can be maintained by compensating the lagging head with a leading eye. When the object is moving fast, however, the phase difference between the head and eyes tends to disrupt smooth tracking [45]. Thus, ultimately, skilful visual tracking has to rely on prospective control of both eyes and head, but initially it is sufficient that one of the modes of control is predictive.

Box 1. Development of prospective control of posture

Gravity is a potent force and when body equilibrium is disturbed, posture becomes quickly uncontrollable. Therefore, any reaction to a balance threat has to be very fast and automatic. Several reflexes have been identified that serve that purpose. However, disturbances to balance are better handled in a prospective way, because then there is no need for emergency reactions and ongoing actions can continue. Developing such prospective control is of crucial importance for action development. Barela, Jeka and Clark [39] studied how infants used a supporting contact surface (a handrail) during the acquisition of upright stance. They found that both body sway and the forces applied to the contact surface decreased as infants gained experience of upright stance. Furthermore, the youngest infants applied forces to the handrail as a reaction to their body sway whereas older infants applied forces to the handrail in *anticipation* of body sway.

Another threat to balance is one's own movements. To maintain balance during limb movements, the reactive forces that they induce must be compensated ahead of time. Witherington *et al.* [40] examined the early development of anticipatory postural activity in support of a pulling action when standing. The task required infants to open a cabinet drawer to retrieve toys while a force resisting the pulling action was applied to the drawer. Before each trial a toy was placed in the drawer, enticing the infant to pull open the drawer to retrieve the toy. Displacements of the drawer, movements of the head and trunk, and activity of both gastrocnemious and biceps muscles were measured. It was found that the proportion of pulls involving anticipatory activity in the gastrocnemius muscles progressively increased between 10 and 17 months of age. The emergence of independent walking in these infants coincided with marked increases in anticipatory postural adjustments relative to pull onset. The frequency of postural adjustments initiated within 500 ms of, and persisting after, the pull onset increased from less than 40% of trials in the pre-standing infants to over 80% in the walking infants.

When infants begin to reach successfully for objects they will also catch moving ones. Infants catch moving objects by initiating arm and hand movements before the object is within reaching distance, aiming ahead of the object's current position to a place where the paths of the object and the hand can intersect [46,47]. Later studies have generalized these findings to include several different motion trajectories [48–50]. However, when the direction of motion was perturbed, infants persisted in reaching for the object at the extension of the previous trajectory [49].

Representing moving objects

From about 4 months of age, infants predictively track an object moving on a linear path behind an occluder by shifting gaze to the reappearance position just before the object arrives there (see Box 3). This ability was found to be strongly correlated ($r = 0.85$) with smooth pursuit skill [51]. This is especially interesting because the gaze shift over the occluder is saccadic. Therefore, it is not the mode of tracking that unites these two tasks, but their prospective nature. Success on both tasks relies on forming predictive models of what is going to happen next. These

Box 2. The development of smooth pursuit

In a series of experiments we measured eye movements, together with EOG and head movements, in unrestrained infants as they tracked a 'happy face' oscillating sinusoidally in front of them at frequencies between 0.2 and 0.4 Hz [41–43]. The trajectory covered 48 deg of visual angle. In these longitudinal studies we found that the improvement in smooth-pursuit tracking was very dramatic and consistent between subjects. Individual infants went from almost no smooth pursuit to adult-like performance in just a few weeks (Figure I).

Some of the infants demonstrated adult gains as early as 10 weeks of age. Such rapid development strongly suggests that the ability for predictive tracking is a result of new connections being established in the central nervous system rather than something that the infant learns from experience. The smooth pursuit in this situation was always predictive. Even when it was insufficient and had to be supplemented with saccades, the smooth part was well timed relative to the head-slip (object motion – head motion).

We also tested 5-month-old infants with an object oscillating at 0.6 Hz, a frequency at which the smooth pursuit of adults typically begins to deteriorate [41]. We found that infants could track this object and that the tracking was predictive. Finally, we tested infants with motion of triangular waveform, that is, the object moved with constant velocity over the whole trajectory and reversed direction abruptly at the end points of it [41]. In contrast to the findings with sinusoidal motion, infants' eye movements lagged this motion by about 200 ms at every reversal. At 5 months of age the lag had diminished but the timing was still inferior to the tracking of the sinusoidal motion. This suggests that the predicted object location is an extrapolation based on the just-seen motion.

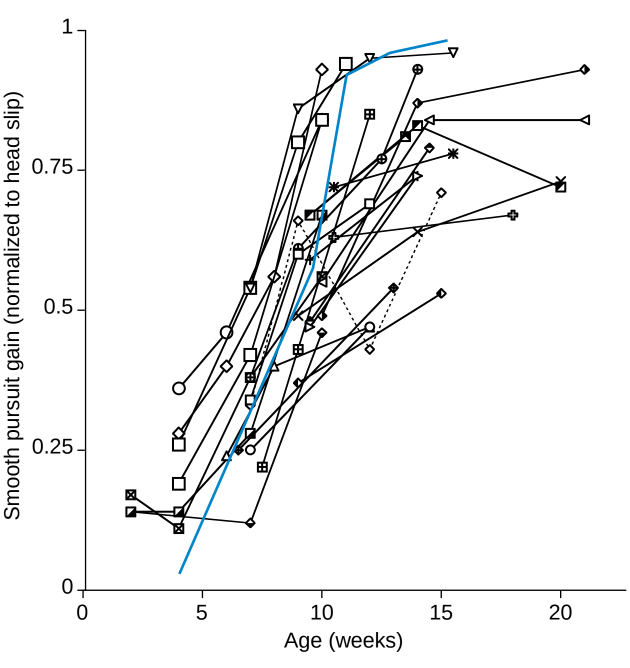

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Figure I. The gain in smooth-pursuit eye tracking of 26 infants from three different studies followed longitudinally over parts of the first 5 months of life (adapted from [41–43]). As a comparison, the development of sensitivity to direction of motion is indicated by the blue line (data from [44]).

models preserve the spatio-temporal properties of the object motion; they are not just confined to linear motion. From at least 6 months of age, infants correctly predict where an object occluded over a quarter of its circular trajectory will reappear [52].

Development of brain mechanisms involved in action control

Because predictive control is such an important aspect of action, several parts of the brain are engaged in solving such problems. On the sensory side, it is evident that the visual system compensates for transmission delays [53]. The cortical MT/MST area is important because it provides information about motion and change (e.g. of size and form). The emergence of smooth-pursuit eye movements (Box 2) and sensitivity to motion direction [44] indicate that this area is functional at around 2 months of age. For representing motion over occlusion, structures in the posterior parietal cortex [54], the prefrontal cortex [55] and the temporal cortex [56] are engaged in primates.

The cerebellum is rarely discussed in the context of motor development, but recent research suggests that the cerebellum is important for predictive motor control [57,58]. At birth, the human cerebellar cortex has a well-established architecture with, for example, all the Purkinje cells present [59] and climbing fibers that make contact with the cell bodies. It is therefore possible that the cerebellum is involved in the construction of movements at that time. The emergence of predictive models in early development might also include the establishment of networks between the posterior parietal cortex and the cerebellum [60]. The cerebellum is also crucially involved in motor learning [61] and should also for this reason be of great importance for motor development.

Conclusions

The basic insight that movements are organized as actions has important consequences, not only for the understanding of motor development, but also for the understanding of other aspects of development. Perceptual development is determined by the action capabilities of the child and what objects and events afford in the context of those actions [36]. Cognitive development has to do with expanding prospective control over and above the information available at any point in time by using rules and representations of events to guide actions. Action development, however, has to be understood in a still wider context. We need to relate our own actions to the actions of other people to develop a theory of mind and for learning new actions. Recent research shows that we spontaneously perceive the movements of other people as actions [6], that specific areas in the brain encode our own and other people's actions alike [9–11,62], and that this forms a basis for learning by imitation [27,63,64]. However, it is equally important to distinguish between the actions of our own and those of others [27], and recent research has identified brain areas specifically devoted to solving this problem [65]. Although there has been much progress in the

Box 3. The development of predictive tracking of temporarily occluded objects

The view of an object that moves in a cluttered environment is frequently interrupted as it passes behind other objects. Visual tracking has to overcome such periods of non-visibility, by shifting gaze to the point of reappearance and preparing to track the object again there. These preparations have to be guided by some kind of representation that preserves the spatio-temporal continuity of the occluded motion instead of just being geared to sensory information. Recent research using habituation [66] and visual tracking [51,67] indicate that 4-month-old infants can represent temporarily occluded objects.

In a study of 39 infants [51] we examined the emergence of this ability from 7 to 21 weeks of age, using the set-up described in Box 2. The object (a happy face) oscillated at 0.25 Hz according to a sinusoidal or a triangular wave function over a trajectory covering 50 deg of visual angle, and was occluded at the centre of its trajectory for 300 ms. Each trial was 20 s duration and included 10 occlusion events. The results showed that 7–9-week-old infants had no idea where or when the disappearing object would reappear (Figure Ia). Their gaze remained at the occluder edge (the point of disappearance) almost 1 s after the object had reappeared on the other side. The 17-week-olds (Figure Ib), however, tended to predict the reappearance after having seen a few occlusions. Learning over single trials was impressive (see Figure Ic) at all ages. The younger infants showed a decrease in reaction time and the older ones became predictive over a trial. The fact that the younger infants became more aware of the reappearing object with experience over a trial suggests that they also acquired some kind of representation of the occluded object. This representation might, however, be too weak to compete for attention with the visible occluder. Therefore, it is possible that younger infants perform better in a situation where an object gets temporarily invisible because of blackout rather than occlusion [68,69]. Six-month-old infants' visual tracking and reaching for a moving object that gets temporarily occluded provides support for this idea [69,70]. The infants tracked predictively an object over occlusion but reaching was totally interrupted. When the non-visibility was produced by blackout instead of occlusion reaching performance was much less impaired and recovered more rapidly.

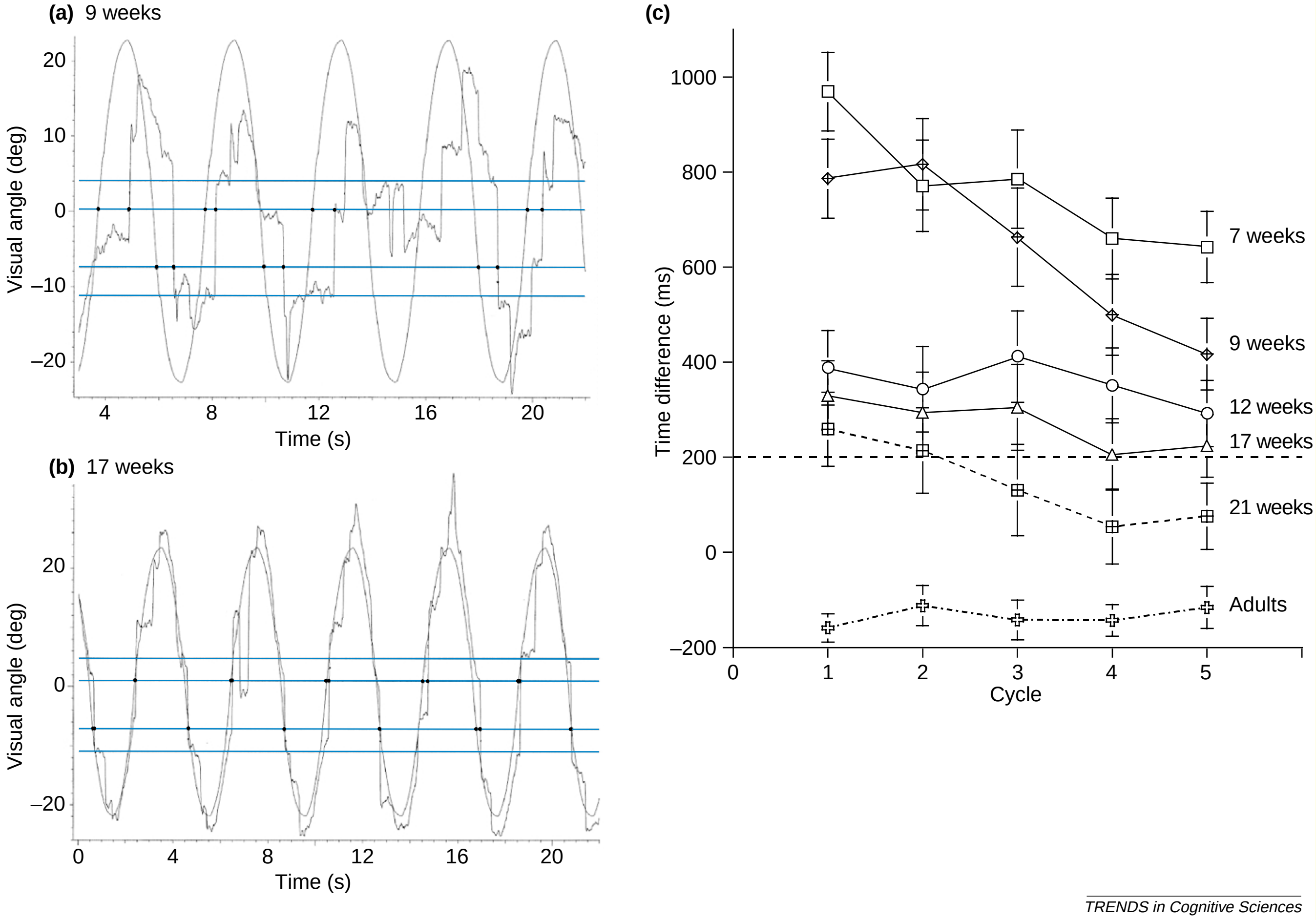

Figure I. **(a)** A 9-week-old infant's gaze movements plotted together with the object motion for single trials, with central occlusion of the object. The graph depicts the event over time (horizontal axis) and space (vertical axis). The outer horizontal lines in the figures signify the occluder boundaries. The inner horizontal lines signify the position of the object marker when the object was totally occluded. **(b)** The same plot for a 17-week-old infant, showing the improvement in predictive tracking of the occluded object (redrawn with permission from [51]). **(c)** The average time differences (ms) and standard errors between object and gaze reappearance at each cycle of the centrally occluded trials in the experiment in [51]. The dotted line corresponds the minimum time required for adults to program a saccade to an unexpected event (200 ms).

understanding of the development of movements as actions, there are still many questions to be addressed (see Box 4).

Box 4. Questions for future research

- There are many unanswered questions related to the development of children's prospective control of action. One striking feature is how smooth and continuous children's movements are and how they are geared to external events. What kinds of sensory information are such movements based on at different ages? How does the ability to represent forthcoming events develop?
- The role of motivation is an important but neglected field of study in motor development. Do motives precede or do they simply accompany important transitions in motor development? To what degree can motivational factors in perception and action be accounted for in terms of an instinct to explore the opportunities provided by the environment and the acting self?
- Although it is quite evident that young children are rapid learners, the exact role played by learning in motor development is yet to be determined. Motor learning in adults is very resistant to forgetting; is this also true for infants? Different kinds of motor learning also need to be explored; for example, the role of imitation in learning new actions.
- How is prospective control related to brain function? Although some of the brain areas important for adult motor control have been identified, their importance for the development of action is still unclear. What kinds of changes in the brain are associated with important advances in the control of actions such as the onset of smooth pursuit, the ability to guide action over periods of non-visibility, and the ability to construct efficient and continuous movements? The solution of these problems calls for at least two kinds of studies: brain imaging in parallel with behavioural measurements, and studies of children with brain pathologies.
- For a full understanding of action development, it is important to know how different modes of action are established. This calls for studies of their development before they become fully functional. For instance, functional reaching does not emerge until about 4 months of age. Before that time, component abilities emerge, such as binocular space perception, postural control, and motivation to reach. How do these abilities relate to each other in the pre-reaching period and in what ways do they determine the emerging skill?

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