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Development of Anticipatory Orienting Strategies During Locomotor Tasks in Children

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GRASSO, R., C. ASSAIANTE, P. PRÉVOST AND A. BERTHOZ. *Development of anticipatory orienting strategies during locomotor tasks in children*. NEUROSCI BIOBEHAV REV **22**(4) 533–539, 1998.—Some basic problems related to the development of goaldirected locomotion in humans are reviewed here. A preliminary study is presented which was aimed at investigating the emergence of anticipatory head orienting strategies during goal-directed locomotion in children. Eight children ranging from 3.5 to 8 years had to walk along a 90° right corner trajectory to reach a goal, both in light and in darkness. The instantaneous orientation in space of the head, trunk, hips and left foot antero/posterior axes was computed by means of an ELITE four-TV camera, 100 Hz system. The results showed that predictive head orienting movements can occur also in the youngest children. The head starts to rotate toward the goal before the corner point of the trajectory is reached. In children, the head peak rotation coincides with the trajectory corner while in adults the peak is attained before. In children, the walking speed is largely decreased in darkness. The results suggest that feedforward control of goaldirected locomotion appears very early in gait development and becomes increasingly important afterwards. © 1998 Elsevier Science Ltd. All rights reserved.

Development Orientation Goal-directed locomotion Anticipation Steering Feedforward control Humans

DEVELOPMENT OF REFERENCE FRAMES FOR GOAL-ORIENTED LOCOMOTION

FROM 9 TO 10 MONTHS, a sort of cognitive revolution must occur when an infant's horizons are expanded by the acquisition of self-initiated, self-controlled locomotion. The development of goal-oriented locomotion mainly implies three abilities: localizing of the visual target, controlling locomotor performance and appropriately organizing the visuo-motor interface. At the beginning, the young infant localizes itself with respect to the physical environment by using an egocentric frame of reference. Piaget argued that action is organized with respect to the child's own movements (37) and spatial localization is carried out with respect to the child's own body position (38). Also, 4- to 6-year-old children belong to this stage. Successively, around 7-8 years, the egocentric mode of representation tends to be abandoned while the child's position and movements begin to be organized with respect to fixed elements of the external environment. Lastly, from 9-10 years onwards, children become capable of building true exocentric topographic representations. In blind children, autonomous locomotion takes place later than normal children (3,31). An absence of early visual experience induces a preferential egocentric mode of spatial representation in blind children (32). In contrast, early visual experience (between the first 12th and 18th months of life) seems sufficient to allow for the exocentric mode (32,1). Whatever is the selected reference frame, it needs to be maintained as stable for allowing the localization and reaching of the selected goals. Recent studies have shown that during the first 3-4 years of independent walking the head is progressively stabilized relative to space (5,6,27). These observations corroborated the hypothesis, originally introduced by Pozzo et al. (41), that head stabilisation facilitates the interpretation of external (mainly visual) and internal (inertial and proprioceptive) cues during locomotion. Such cuerelated afferent signals can thus be used to assess the instantaneous relationship between the body and the surrounding environment.

NON VISUAL CUES IN GOAL-ORIENTED LOCOMOTION

For the control of locomotion, vision cannot be thought of as the only source of spatial information. Besides its recognized (and thoroughly investigated) functions in regulating and stabilising gaze, posture and movements, the vestibular system has long been suggested to significantly contribute to the orientation and localisation of the

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body in space during displacements (54,9,11,40,35) in the so-called path-integration behaviour. Ascending pathways conveying multi-sensory (vestibular, proprioceptive and visual) information attain specific areas in the brain related to representation of space (21,51). In recent years, a bulk of information has been accumulated about the existence of neural networks responding to head direction in an allocentric reference frame-the so-called 'head direction cells' in the thalamus and postsubiculum of rats (34). Among the properties of some subtype of these neurones there is a responsiveness to head angular velocity which led some researchers (13) to hypothesize the existence of a predictive thalamo-cortical circuit sensing future heading of locomotion. The afferent pathways and the cortical areas dedicated to motion perception are now identified also in humans (14,52) and cells with properties similar to those of the head direction cells in the rat have been recently described also in primates (Rolls, unpublished observations). In adult humans, it has been recently reported that changes of head direction systematically anticipate changes in the direction of locomotion along circular paths (by about 200 ms) (19). Also, adults instructed to walk along a 90° corner trajectory toward a target consistently turn their head in the direction of the intended walk long before (about 1 s) they modify the body trajectory (20). A similar result has been found by Land and Lee (26) in car drivers approaching a road bend. All these observed behaviour resulted from a coordination of head and eye movements supporting gaze orientation (19,25,42).

THE EMERGENCE OF ANTICIPATORY STRATEGIES

In general, anticipation is considered a crucial turning point when acquiring skills (17). Anticipatory mechanisms, building prediction of future sensory and motor events, have been demonstrated in adults during many activities (pursuit eye movements (10), reaching hand movements (24), postural synergies (22) and gait initiation (33)). Anticipatory mechanisms during pursuit eye movements seems mature in infants around 1 year of age (47,49). Some anticipatory mechanisms based on coordination of vision and reaching have been demonstrated in young infants (53). Anticipatory displacements of the center of pressure in gait initiation have been shown to build up between 1.5 and 2.5 years of age (15,28,30). Up to now, however, very little attention has been paid to the development of anticipatory head orienting strategies during locomotor tasks. Some studies in young children (2,44,45) have reported anticipatory head orienting movements in various tasks of spatial localization in response to the appearance of an attractive stimulus. This behaviour emerges very early in the prehensive space (around 6 months) and between 11 and 16 months of age in the locomotor space. In locomotion, because of the presence of important biomechanical delays, anticipating the direction one intends to go is essential in view of avoiding obstacles or of following path constraints (36). In general, anticipation implies the presence of feedforward control of movement (43,46) and it is here proposed to analyse the development of anticipatory strategies to understand the general mechanisms of the implementation of feedforward control during childhood.

A PURPOSE STUDY ADDRESSING THE EMERGENCE OF ANTICIPATORY CONTROL OF GOAL-DIRECTED LOCOMOTION

In a preliminary study presented below we aimed at investigating the emergence of anticipatory head orienting strategies during goal-directed locomotion. Eight healthy children, from 3.5 to 8.5 years of age, comprising five girls and three boys, participated in the study. They were asked to walk from a starting-point to an end-point (where the experimenter was waiting) along a right corner trajectory (90°, Fig. 1) in two conditions: first with eyes open (LIGHT) and second while wearing blindfolds (DARK). Each child had to perform four consecutive trials in each condition except for youngest children (< 4 years) who, despite the presence of their parents, refused to perform in

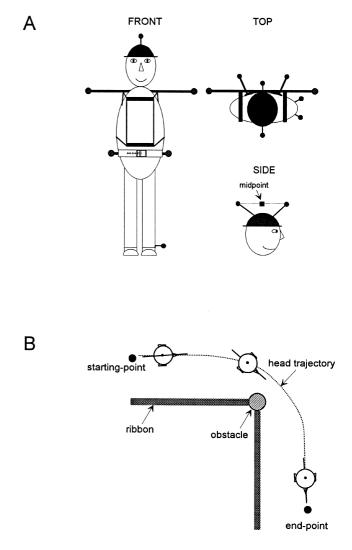


FIG. 1. Experimental setup. The experiments were performed in a large room (5.1 \times 6.2 \times 3.4 m length/width/height) equipped with a four-camera (100 Hz) ELITE system. (A) The position of the markers from three viewpoints is shown. Note the presence of antennae to increase the intermarker distance. The midpoint between the two head markers was on the yaw rotation axis and it was used to measure head position in space. The final accuracy was 0.3° (root mean square) for head, trunk and hips orientation and about 1° for the foot. (B) Experimental task. The subjects had to reach a target positioned at the end-point of a 90° right corner trajectory. A plastic ribbon placed along the trajectory prevented children from using shortcuts.

darkness. No instruction about speed was provided. The real-time orientation of the head, trunk, hips and left foot antero/posterior axes in the horizontal plane were computed. The direction of locomotion was measured from the tangent to two positions successively occupied by the midpoint between the two head markers (19). The instantaneous difference between head orientation and locomotion direction is called θ . For each locomotor trajectory the corner position was computed as that corresponding to the point where curvature attained a maximum. Starting back and forth from this turning point, ensemble averages of individual trajectories (mean of *x*, *y* coordinates, instant by instant) and orientation angles (±1SEM) from different trials and/or from different subjects were computed.

THE DEVELOPMENT OF A STRATEGY TO REACH THE GOAL

The results of this experiment must be compared with

those from a matched study conducted on six adults (two trials per each subject). Figure 2 shows the mean trajectory and head orientation displayed by the group of adults compared to the mean from three consecutive trials performed by the youngest child (3.5 years), in the LIGHT condition. The figure clearly shows that head direction anticipates the change of trajectory both in the group of adults and in the child. Anticipatory orientation builds up starting from about 1 s before the turning point is attained. After the turning point the walking direction realigns to head orientation. A similar pattern was observed at least once in all the children participating in the study.

Table 1 shows the occurrence time of θ peak relative to the subjective corner position for all eight subjects and four trials. Of the children younger than 5.5 only one case shows a consistent time lead. Time lead is also displayed by one of the 5.5-year-old children and by all of the children older than 5.5. The difference in time lead between the group

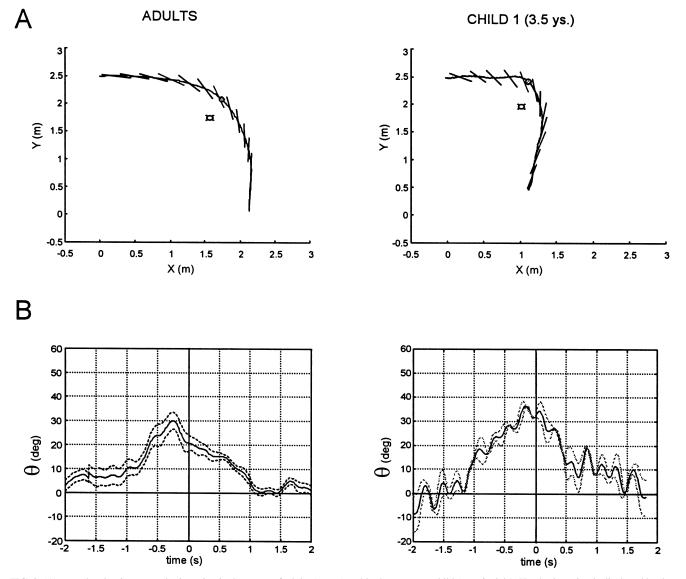


FIG. 2. (A) mean head trajectory and orientation in the group of adults (N = 6) and in the youngest child (N = 3 trials). Head orientation is displayed by the short straight segment, at a convenient time resolution, along the walked path. The coordinates of the turning point (dashed circle) result from averaging of the coordinates of the points where curvature attained a maximum on individual trajectories. The position of the obstacle is also indicated (solid circle with ticks). (B) Time course of θ angle (i.e., the head deviation relative to the walking direction) from the time occurrence of the turning point (which corresponds to 0). Anticipatory orientation develops about 1 s before the turning point and reaches a peak amplitude of 30–40°.

TABLE 1 TIME OCCURRENCE OF θ PEAK RELATIVE TO THE TRAJECTORY CORNER POSITION

	Subject 1 (3.5 years)	Subject 2 (3.5 years)	Subject 3 (4 years4)	Subject 4 (5.5 years)	subject 5 (5.5 years)	Subject 6 (6.5 years)	Subject 7 (8 years)	Subject 8 (8 years)
Trial 1	-0.10	0.88	0.12	0.33	-0.13	-0.01	-0.04	0.08
Trial 2	-0.14	[0.36]	0.10	0.30	-0.17	-0.02	-0.02	-0.11
Trial 3	-0.13	[0.31]	[-1.74]	0.35	-0.10	[1.13]	-0.06	[-0.15]
Trial 4		[-1.76]	0.12	0.36	-0.18	-0.08	-0.07	-0.05
Mean	-0.12	0.88	0.12	0.34	-0.15	-0.04	-0.05	-0.03
SD	0.02	-	0.01	0.03	0.04	0.04	0.02	0.10

Values from all subjects and trials. Negative values indicate a time lead. Numbers between square brackets are not included in the subject mean as they refer to trials where θ displayed an oscillatory step-related pattern with no relation with the corner position. The difference between the younger children group (< 4 years) and the older group (> 4 years) is not significant. The peak value does not correspond to the bulding up of the anticipatory orienting movement.

of adults and that of children was significant (unpaired Student's, t = 2.37 d.f. = 12, p = 0.034, Fig. 3). On the contrary, there is no difference between groups in the amplitude of θ peak (36 ± 11.2° vs 34 ± 11.4°, n.s.).

From these results we can conclude that anticipatory head orienting movements during locomotion are present at a very early stage of gait development. However, while in adults, anticipatory head motion has been found to be very reproducible across repeated trials, the opposite seems true for children, especially for the youngest ones. This steering behaviour has been previously described as a 'go where you look' strategy (19), meaning that one gazes into the new direction he/she wants to undertake before guiding his/her body there. It may be suggested that the behaviour is not peculiar of locomotion but it reflects the maturation of general orientation strategies demanding foveal vision and gaze dynamic control. These strategies are probably developed during the first months of selfproduced forms of experience such as crawling (12), or even earlier, in spatial search behaviour. Thus, orientation control strategies on the basis of which feedforward control of locomotion will be developed, may be put under test very early in the human life span. An interesting observation was that the anticipation time interval of the peak of θ angle was

consistently longer in adults, suggesting that the prediction at the basis of feedforward control moves farther in the future with age.

THE DEVELOPMENT OF STEERING MOVEMENTS

Figure 4 shows the average time course of all recorded body segment orientation for two children aged 3.5 and 5.5 years respectively. It can be noticed that in the younger child head motion is not preceding the motion of the other body segments, rather it follows them. On the contrary, the older child displays a clear cut anticipation of head motion relative to the rest of the body. This latter child is the youngest one in whom we could see such an anticipation to occur in a stable fashion across the repeated trials. In adults, head motion consistently anticipated trunk orientation changes by 0.44 s with eyes open (the θ peak for the head preceded the corner position of 0.24 \pm 0.06 s while the trunk followed the corner position by 0.20 \pm 0.13 s).

Therefore, while in adults changes in instantaneous head direction in space result from neck rotations, in children there was an attitude to lump head and trunk in

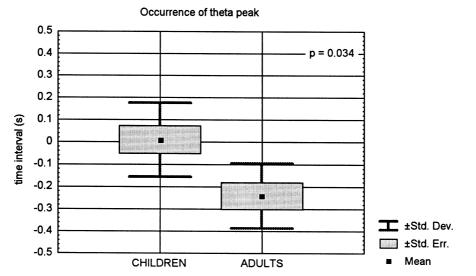


FIG. 3. Box and line plots represent the average (SEM and SD) of time occurrence of θ peak relative to the trajectory turning points from the group of adults (N = 6) and children (N = 8). The peak anticipates the occurrence of the turning point in adults, but not in children. Time lead values are -0.24 ± 0.06 and 0.03 ± 0.03 s, respectively.

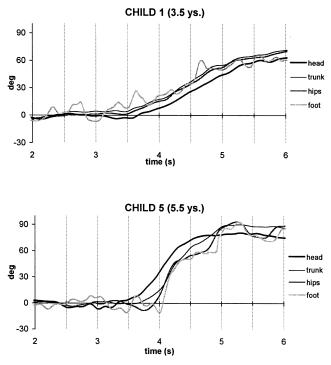


FIG. 4. Time course of the instantaneous orientation of the head, trunk, hips and left foot antero/posterior axis during the path for two children of different age (LIGHT condition). Curves represent the average from three and four trials respectively. Head orientation is lagging behind the orientation of the other body segments in the younger child whereas it leads on the other segments in the older child.

a single mechanical unit (as shown in Fig. 4). The two 3.5year-old children showed delayed head movements relative to the other recorded segment as we would expect if the head were passively coupled to the trunk. It is worth noting that the foot, the hips and the trunk directions showed simultaneous changes in most children (as in the child of Fig. 4), suggesting that an immediate transfer of the leg jerk to the rest of the body occurs. These observations are consistent with the use of an 'en bloc' movement strategy as it was shown to happen in young children during balance locomotor tasks (7). Such a behaviour might be aimed at decreasing the number of degrees of freedom to be simultaneously controlled during the movement. The results suggest a developmental sequence from an en bloc operation of the body to an articulated operation with maturation as recently proposed in an ontogenetic model of the organisation of postural dynamic balance (7). The model assumes an alternation between two main modalities: one which follows a caudo-cephalic gradient and is characteristic of early standing and locomotor experience, and another one, which follows the opposite anatomical gradient and pertains to mature postural and locomotor control. The same anatomical gradient followed by the development of postural control seems to be followed by the dynamic control of goal-oriented locomotion. Also the data from Table 1, described in the preceding section, seem to fit nicely this model and confirm that the age cross-over must occur around 5/6 years of age.

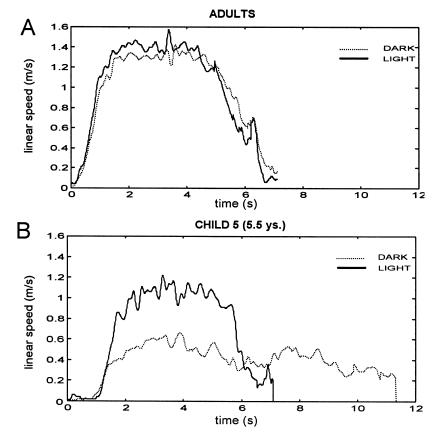


FIG. 5. (A) Average linear speed in LIGHT and DARK condition in the group of adults (N = 6). (B) average linear speed in LIGHT and DARK condition for child 5 (N = 4). Note the dramatic decrease of speed when the child was wearing blindfolds.

THE DEVELOPMENT OF THE VISUO-MOTOR INTERFACE

Figure 5 shows the effect of the experimental conditions on the walking speed in the group of adults (upper panel) and in a 5.5-year-old child (lower panel). Upper curves represent the mean from the group of six adults, whereas lower curves result from averaging five trials (per each condition) from the same child. Contrary to adults, in whom there was a small difference between the two conditions $(1.33 \pm 0.16 \text{ m/s } vs 1.21 \pm 0.21 \text{ m/s in LIGHT}$ and DARK respectively) the children older than 5 (the youngest refused to perform in darkness) decreased their speed by 37% when performing in darkness (from 0.95 \pm 0.14 m/s in LIGHT to 0.60 \pm 0.23, in DARK).

Such an impressive effect of the visual condition on walking speed in children and the fact that youngest children absolutely refused to perform in darkness seems to fit with the findings of above-mentioned studies on the absence of early visual experience (3,31). A net reduction in locomotor speed has been previously observed in children required to walk on a narrow support with balance difficulty (5), but in the present study there was no path restriction which could directly impair balance control. Studies conducted on visually impaired adults and children reported a decrease of locomotor speed with respect to healthy individuals, associated with a longer duration of stance phases (16,39). Residual visual cues largely improved locomotor speed of visually impaired children (39). It can be hypothesized that the use of cues alternative to vision is awkward to children, as they do not have enough time to learn how to correlate self motion to optic flow to generate a stable internal representation of the environment in darkness. The affordance of peripheral flow for maintaining stability (29,50) appears to be differentiated from the affordance of central radial outflow for steering in adults and children over two years, but the differentiation may not be complete, and it may depend on exploratory locomotion and practice in walking (48). The observed effect of the visual condition could also be explained by a greater difficulty for children to consider their motion relative to space in an objective, non-egocentric reference frame. It has been recently shown (4) that updating the internal representation of the outer space during locomotion, involves different computational procedures depending on whether an internal viewer-centred or an external objectcentred frame of reference is selected. Probably, the development of these cognitive procedures requires long-term locomotor practice.

CONCLUSION

Some authors dissociated two types of anticipatory mechanisms involved during goal-directed locomotion: (1) preparatory head (gaze) orienting movements toward the goal which precede locomotion; (2) integrative or predictive changes of head orientation which occur during the locomotor trajectory (18,28,33). The latter mechanism requires the development of a true dynamic feedforward control which was the main interest of the purpose study. It has been reported that 'preparatory' movements mature earlier than 'predictive' movements in gait initiation in children (8). Certainly, the large intra-individual variability displayed in the present study by children can be interpreted as an evidence that the feedforward control is not yet definitely acquired and is not stable enough to show up systematically. Early emergence and later stabilisation of adult-typical response have been shown in the development of anticipatory mechanisms in gait initiation (8) and in the development of postural adjustments associated with sitting (23). The present data provide some evidence that feedforward control of locomotor goal-directed trajectories is increasingly important, from the first years of independent gait onwards. The head seems to become progressively more independent from the trunk and shows predictive movements toward the goal. We suggest that further studies on the development of anticipatory skills would greatly benefit from an accurate kinematic analysis, such as are performed in the present experiment.

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REFERENCES

- 1. Acredolo, L.P., Developmental changes in the ability to coordinate perspectives in a large scale space. *Dev. Psychol.*, 1977, **13**, 1–8.
- 2. Acredolo, L.P., Development of spatial orientation in infancy. *Dev. Psychol.*, 1978, **14**, 224–234.
- Adelson, E. and Fraiberg, S., Gross motor development in infants blind from birth. *Child. Dev.*, 1974, 45, 114–126.
- Amorim, M.A., Glasauer, S., Corpinot, K., Berthoz, A. Updating an object's orientation and location during nonvisual navigation: a comparison between two processing modes. *Perception & Psychophysics*, 1997, **59**, 404–418.
- Assaiante, C. and Amblard, B., Peripheral vision and age-related differences in dynamic balance. *Hum. Mov. Sci.*, 1992, **11**, 533– 548.
- Assaiante, C. and Amblard, B., Ontogenesis of head stabilization in space during locomotion in children: Influence of visual cues. *Exp. Brain Res.*, 1993, **93**, 499–515.
- Assaiante, C. and Amblard, B., An ontogenetic model for the sensorimotor organization of balance control in humans. *Hum. Mov. Sci.*, 1995, 14, 13–43.

- Assaiante, C., Development of locomotor balance control in healthy children. *Neurosci. Biobehav. Rev.*, 1998, 22, 527–532.
- 9. Barlow, J.S., Inertial navigation as a basis for animal navigation. *Theor. Biol.*, 1964, **6**, 76–117.
- Barnes, C.A., Foster, T.C., Rao, G. and McNaughton, B.L., Specificity of functional changes during normal brain aging. *Ann. N.Y. Acad. Sci.*, 1991, 640, 80–85.
- Beritoff, J.S. Spatial Orientation in Man. In: Liberson, W.T., ed. Neural Mechanisms of higher vertebrate behavior. Boston: Little, Brown and Company; 1965:137–157.
- Bertenthal, B.I., Origins and early development of perception, action, and representation. Ann. Rev. Psychol., 1996, 47, 431– 459.
- Blair, H.T. and Sharp, P.E., Anticipatory head direction signals in anterior thalamus: Evidence for a thalamocortical circuit that integrates angular head motion to compute head direction. *J. Neurosci.*, 1995, **15**, 6260–6270.
- Bottini, G., Sterzi, R., Paulesu, E., Vallar, G., Cappa, S., Erminio, F., Passingham, R.E., Frith, C.D. and Frackowiak, R.S.J., Identification of

the central vestibular projections in man: a PET study. *Exp. Brain Res.*, 1994, **99**, 164–169.

- Brenière, Y., Bril, B. and Fontaine, R., Analysis of the transition from upright stance to steady state locomotion in children with under 200 days of autonomous walking. *J. Motor Behav.*, 1989, 21, 20–37.
- Clark-Carter, D.D., Heyes, A.D. and Howarth, C.I., The gait of visually impaired pedestrians. *Hum. Mov. Sci.*, 1987, 6 (3), 277–282.
- Flowers, K. Discussion: identifying crucial elements in skills. In: Colley, A.M.; Beech, J.R., eds. Cognition and action in skilled behaviour. Amsterdam: Elsevier; 1988:311–313.
- Gahéry, Y., Associate movements, postural adjustments and synergies: some comments about the history and significance of three motor concepts. *Archs Ital. Biol.*, 1987, **125**, 345–360.
- Grasso, R., Glasauer, S., Takei, Y. and Berthoz, A., The predictive brain: Anticipatory control of head direction for the steering of locomotion. *NeuroReport*, 1996, 7, 1170–1174.
- Grasso, R., Ivanenko, Y., Prevost, P., Berthoz, A. Vestibular and visual involvement in head anticipation of direction of locomotion. J. Vestib. Res. 6–4s: s2 (abstract), 1996.
- Grüsser, O.J., Guldin, W.O., Harris, L., Lefèbre, J., Pause, M. Cortical representation of head-in-space movement and some psychophysical experiments on head movement. In: Berthoz, A.; Graf, W.; Vidal, P-P., eds. The Head–Neck Sensory Motor System. 79ème ed. New York, Oxford: Oxford University Press; 1992:497.
- Gurfinkel, V.S., Lipshits, M.I. and Lestienne, F.G., Anticipatory neck muscle activity associated with rapid arm movements. *Neurosci. Letts*, 1988, 94, 104–108.
- 23. Hadders-Algra, M., Brogen, E. and Forssberg, H., Ontogeny of postural adjustments during sitting in infancy: variation selection and modulation. *J. Physiol. (Lond.)*, 1996, **493.1**, 273–288.
- Jeannerod, M., Arbib, M.A., Rizzolatti, G. and Sakata, H., Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends. Neurosci.*, 1995, 18, 314–320.
- Land, M.F., Predictable eye-head coordination during driving. *Nature*, 1992, **359**, 318–320.
- Land, M.F. and Lee, D.N., Where we look when we steer. *Nature*, 1994, 369, 742–744.
- Ledebt, A., Bril, B. and Wiener-Vacher, S., Trunk and head stabilization during the first months of independent walking. *NeuroReport*, 1995, 6, 1737–1740.
- Ledebt, A., Bril, B. and Brenière, Y. The preparation for movement: acquisition of prospective control in walking. Proceedings of the European Conference on Cognitive Sciences, 4–7 April 1995, Saint Malo, le Chesnay: INRIA, 145–154, 1995.
- Lee, D. and Aronson, E., Visual proprioceptive control of standing in human infants. *Percept. Psychophys.*, 1974, 15, 529–532.
- Lepers, R. and Brenière, Y., The role of anticipatory postural adjustments and gravity in gait initiation. *Exp. Brain Res.*, 1995, 107, 118– 124.
- 31. Mellier, D. and Jouen, F., Remarques à propos des déplacements chez le bébé aveugle. *Psychologie Française*, 1986, **31**, 43–47.
- Millar, S., The utilisation of external and movement cues in simple spatial tasks by blind and sighted children. *Perception*, 1979, 8, 11–20.
- Massion, J., Movements, Posture and Equilibrium: interaction and coordination. *Progr. Neurobiol.*, 1992, 38, 35–56.
- 34. McNaughton, B.L., Barnes, C.A., Gerrard, J.L., Gothard, K., Jung,

M.W., Knierim, J.J., Kudrimoti, H., Qin, Y., Skaggs, W.E., Suster, M. and Weaver, K.L., Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *J. Exp. Biol.*, 1996, **199**, 173–185.

- Mittelstaedt, M.L. and Glasauer, S., Idiothetic navigation in gerbils and humans. Zoologische Jahrbuch Physiologie, 1991, 95, 427–435.
- Patla, A.E., Prentice, S.D., Robinson, C. and Neufeld, J., Visual control of locomotion: sttrategies for changing direction and for going over obstacles. J. Exp. Psychol., Hum. Percep. Perform., 1991, 17, 603–634.
- Piaget, J.; Inhelder, B.; Szeminska, A. La géométrie spontanée de l'enfant. Paris: P.U.F.; 1948:516.
- Piaget, J.; Inhelder, B. The child's conception of space. New York: Norton; 1967.
- 39. Portalier, S. and Vital-Durand, F., Locomotion chez les enfants malvoyants et aveugles. *Psychologie Française*, 1989, **34**, 79–85.
- Potegal, M. Vestibular and neostriatal contribution to spatial orientation. In: Potegal, M., ed. Spatial abilities. London: Academic Press; 1982:361–387.
- Pozzo, T., Berthoz, A. and Lefort, L., Head stabilization during various locomotory tasks in humans. I. Normal subjects. *Exp. Brain Res.*, 1990, 82, 97–106.
- 42. Prevost, P. Analyse du mouvement de la tête et du tronc dans la locomotion autour d'un obstacle. Mémoire de D.E.A en Biomécanique et Physiologie du mouvement. Université de Paris—Sud Orsay; 1996.
- Riehle, A., Kornblum, S. and Requin, J., Neuronal coding of stimulus– response association rules in the motor cortex. *NeuroReport*, 1994, 5, 2462–2464.
- Rieser, J.J., Reference systems and the spatial orientation of sixmonths-old infants. *Child Dev.*, 1979, 50, 1078–1087.
- Rieser, J.J. and Heiman, M.L., Spatial self-reference systems and shortest-route behavior in toddlers. *Child Dev.*, 1982, 53, 524–533.
- Rosenbaum, D.A., Human movement initiation: specification of arm, direction and extent. J. Exp. Psychol., Gen., 1980, 109, 444–474.
- Roucoux, A., Culee, C. and Roucoux, M., Development of fixation and pursuit eye movements in human infants. *Behav. Brain Res.*, 1983, 10, 133–139.
- Schmuckler, M.A. and Gibson, E.J. The effect of imposed optical flow on guided locomotion in young walkers. *British J. Dev. Psychol.*, 1989, 7, 193–206.
- Shea, S.L. and Aslin, R.N., Oculomotor responses to step-ramp targets by young human infants. *Vision Res.*, 1990, **30**, 1077–1092.
- Stoffregen, T.A., Schmuckler, M.A. and Gibson, E.J., Use of central and peripheral optical flow in stance and locomotion in young walkers. *Perception*, 1987, 16, 113–119.
- Taube, J.S., Goodridge, J.P., Golob, E.J., Dudchenko, P.A. and Stackman, R.W., Processing the head direction cell signal: A review and commentary. *Brain Res. Bull.*, 1996, **40**, 477–484.
- Vitte, E., Derosier, C., Caritu, Y., Berthoz, A., Hasboun, D. and Soulié, D., Activation of the hippocampal formation by vestibular stimulation: a functional magnetic resonance imaging study. *Exp. Brain Res.*, 1996, **112**, 523–526.
- 53. von Hofsten, C., Predictive reaching for moving objects by human infants. J. Exp. Child Psychol., 1980, **30** (3), 369–382.
- Worchel, P., The role of vestibular organs in spatial orientation. J. of Exp. Psychol. Gen., 1952, 44, 4–y10.