

CHAPTER 6

The development of multisensory balance, locomotion, orientation and navigation

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1. Introduction

This chapter describes development of the sensory processes underlying the movement of our bodies in space. In order to move around the world in an adaptive manner infants and children must overcome a range of sensory and motor challenges. Since balance is a pre-requisite for whole-body movement and locomotion, a primary challenge is using sensory inputs to maintain balance. The ultimate goal of movement is to reach (or avoid) specific objects or locations in space. Thus, a further pre-requisite for adaptive spatial behaviour is the ability to represent the locations of significant objects and places. Information about such objects, and about one's own movement ("self-motion") comes from many different senses. A crucial challenge for infants and children (not to mention adults) is to select or integrate these correctly to perform spatial tasks.

We will first describe the development of balance and locomotion. We will then go on to describe the development of spatial orientation and navigation. Basic spatial orienting (*e.g.*, turning the head to localise multisensory stimuli), which does not require balance or locomotion, is also described in this section. These early-developing orienting behaviours are building blocks for more sophisticated navigation and spatial recall.

We will describe a number of situations in which spatial behaviour in response to multiple sensory inputs undergoes marked changes in childhood before reaching the adult state. Bayesian integration of estimates is a theoretical framework that may accommodate some of these findings. In the concluding section of this chapter

(Section 5), we will describe this framework and highlight its potential for explaining some of the existing developmental findings. However, we will argue that most of the experimental work needed to evaluate the Bayesian explanation still remains to be done.

2. Development of multisensory balance and locomotion

Human balance mechanisms allow us to maintain a positional equilibrium by coordinating internal and external forces on the body. Static balance refers to the maintenance of equilibrium during quiet stance (standing still), whereas dynamic balance refers to the maintenance of equilibrium during movement as, for example, during walking. In line with the focus of available/current research, we will concentrate on static balance. Maintaining balance is vitally important for developing infants and children, because it provides a base on which to build other skills. For example, being able to sit upright allows for reaching; being able to stand without falling over allows for walking. These motor skills in turn permit explorations of the surrounding space and objects. Useful information for balance and locomotion comes from multiple senses. However, development poses a difficult context in which to integrate these multisensory inputs for balance and locomotion, because the child's sensory and motor capabilities are still developing, while her body is also changing in shape, size and mass.

In this review we will separate the sensory inputs used to maintain balance into three functional groupings: visual inputs, vestibular inputs, and information from muscle and joint mechanoreceptors which we term "proprioception". The key visual

information for balance is that which signals relative motion between an observer and their environment. Such movement produces characteristic patterns of change (“optic flow”) in the visual environment (J.J. Gibson 1979). For example, as an observer sways forwards toward an object, the image of that object expands. This characteristic “expansion” pattern therefore signals that the observer is moving forwards and a corrective, backwards sway response may be made. The medial superior temporal area MST plays a prominent role in processing these signals, as do subcortical structures (Billington *et al.* 2010; Wall and Smith 2008). In the vestibular system, the semicircular canals provide information about the rotation of the head whereas the otolith organs signal linear accelerations (Day and Fitzpatrick 2005). This information is processed in the vestibular nuclei and subsequently in higher structures including the cerebellum and cortex (see Angelaki *et al.* 2009). Finally what we term proprioception includes information arising from muscle spindles sensing muscle stretch and similar mechanoreceptors in the joints.

2.1 Multisensory balance development

Many studies suggest that balance control is strongly coupled to visual information very early in infancy. Furthermore, this coupling seems to require little experience of standing or even sitting upright. Children as young as 3 days old make head movements in response to expanding optic flow stimuli, and head movement increases linearly as a function of flow velocity (Jouen *et al.* 2000). Preferential looking also shows that 2 month olds can discriminate global radial expansion patterns from random patterns. Sensitivity to this motion increases during the first year of life (Brosseau-Lachaine *et al.* 2008). The earliest responses may have a subcortical basis

while later responses are likely to recruit cortical visual areas sensitive to global flow patterns, such as MT and MST (Wall *et al.* 2008; Wattam-Bell *et al.* 2010).

--Insert Figure 6.1 about here--

The “swinging room” technique (Lishman and Lee 1973) has been widely used to investigate the balance responses of infants and children (**Fig. 6.1**). Participants stand on a platform inside what appears to be a small room. The walls and ceiling of the room move back and forth independently of the floor, which is fixed. This causes adult participants to sway with the motion of the room. When the room moves towards the participant, creating an expansion pattern (**Fig. 6.1b**), the participant takes this to signal self-motion forwards and corrects their perceived posture by swaying backwards, with the motion of the room. Thus participants became “hooked like puppets” to the motion of the room. The development of this phenomenon in childhood can be characterised by two processes: first, a decrease in the gain of the sway response (older children sway less in proportion to the sway of the room); and second, an increase in the temporal coupling between room motion and body sway.

Sway responses are present very early: sitting 5-month-olds sway in synchrony with the room (Bertenthal *et al.* 1997). Strong sway responses are maintained across the transition from crawling to walking (Lee and Aronson 1974). Indeed, responses to the moving room are produced to a greater degree for infants with crawling or locomotor experience than for less experienced infants of the same age (Higgins *et al.* 1996). Many new walkers respond so strongly to the stimulus that they stumble or fall over. Thus, visual inputs provide stronger inputs to balance at this age than they do in adults. This is still true of 3- to 4-year-old children (Wann *et al.* 1998), though the

falling responses have disappeared by this age. The extent of visually-driven sway decreases rather sharply between 4 and 6 years (Godoi and Barela 2008), indicating a transition away from visual dominance of balance responses which continues through childhood. To understand the exact developmental trajectory of sway gain, the literature would benefit studies which use the same paradigm over a very broad age range, including older children and teenagers. However, available data demonstrate that for children aged 7 to 14 years, the gain of sway to a swinging room is still higher than in adults (Sparto *et al.* 2006; Godoi and Barela 2008).

Alongside the very gradual weakening of responses to visual information, there is a gradual increase in the temporal coupling of room movement and body sway through childhood. Developments in coupling can be seen as early as 5 to 13 months (Bertenthal *et al.* 1997); and continue through mid-childhood. Coherence between room and body sway reaches adult levels by 10 years (Godoi and Barela 2008; Rinaldi *et al.* 2009). This may indicate improvements in muscular control, but could also reflect the refinement of visuomotor mechanisms (Godoi and Barela 2008; Rinaldi *et al.* 2009). This increased coupling may be a general feature of perceptual development, since it is also found using a “haptic moving room” (Barela *et al.* 2003) where the relevant sensory information is haptic rather than visual.

While the swinging room technique allows for the systematic manipulation of visual input, work using platform perturbations has investigated the contributions of visual, proprioceptive and vestibular inputs within one task (Shumway-Cook and Woollacott 1985; Woollacott *et al.* 1987). Children stood with eyes closed on a platform which rotated underfoot to dorsiflex the ankle joint. In these conditions, visual signals are not present and vestibular inputs do not initially signal sway. Only proprioceptive information from the ankle joint indicates that a balance response is

necessary. Children aged 15-31 months did not sway significantly in this situation (Woollacott *et al.* 1987). This result accords with those from the swinging room studies in showing that, for very young children, visual and vestibular inputs are much more effective than proprioceptive inputs in driving balance responses. Similar platform rotations do evoke significant sway responses in children older than 4 years. At this age, where responses to moving visual scenes are also decreasing, proprioceptive information alone becomes sufficient to induce sway (Shumway-Cook and Woollacott 1985).

Further conditions in this study measured the relative contributions of vision and proprioception to balance, asking the children to stand still in four sensory conditions (**Fig. 6.2**). There was no sudden platform perturbation, but different conditions removed reliable visual information, reliable proprioceptive information, neither, or both. Visual information is simply removed by having children close their eyes. Reliable proprioceptive information is removed by making the platform “sway-referenced”; that is, the participant’s sway is monitored and the platform is rotated accordingly, so that the ankle joint always remains at 90°. In this situation proprioceptive information remains present, but is incongruent with other inputs. Reliable vestibular information was available in all conditions.

--Insert Figure 6.2 about here--

Removing visual information caused greater increases in sway for 4- to 6-year-olds than for older children or adults. However, removing reliable proprioceptive information caused even greater increases in sway than removing vision. Removing both visual and proprioceptive information caused dangerous amounts of sway, with

the majority of 4- to 6-year-olds falling over. These results suggest that as for adults, both these sources of information are very important in maintaining balance for children of this age. However, 4- to 6-year-olds are more destabilized than adults under conditions of sensory conflict, for example when the proprioception system signals no movement while the vision and vestibular systems signal movement.

Initial studies found that 7- to 10-year-olds' balance during platform translations was not greatly affected by removing vision (Shumway-Cook and Woollacott 1985). In these respects, 7- to 10-year-olds' performance was very similar to that of adults tested on the same tasks. This indicated weaker visual, and stronger proprioceptive contributions to balance than at younger ages. However, recent work has suggested that fully mature balance responses may not occur until 12 to 15 years (Hirabayashi and Iwasaki 1995; Peterka and Black 1990; Peterson, Christou, and Rosengren 2006). Again, more detailed studies of balance in the late childhood and early teenage years would be valuable in developing a fuller picture of multisensory balance control towards adulthood.

Together the swinging room and platform perturbation experiments suggest an early reliance on visual information. The end of this period and transition away from reliance on vision emerges around 5 years. Sway responses also achieve a tighter temporal coupling to sensory inputs during mid-childhood. However, the longer developmental trajectories of these processes are relatively under-researched.

2.2. Multisensory locomotor development

There are several distinct roles for sensory inputs to locomotion. First, as we have seen, the processing of visual, proprioceptive and vestibular inputs is crucial for balance, and balance in turn underpins locomotion. Indeed, an important achievement

for early walkers is learning to differentiate visual information for walking from visual information for balance. For example, balance can be challenged during walking by moving the room walls. In this situation, experienced walkers are highly influenced by the nature of the walking task (presence / absence of obstacles) as well as by the visual information present for balance. In contrast, more experienced walkers react to balance demands equally well in both navigation conditions (Schmuckler and Gibson 1989).

A further role of sensory inputs in locomotion is allowing the walker to judge properties of the environment, and the position of the limbs. This may be done in the planning phase of a movement, or “online”, during the movement. The development of visual planning in locomotion has been tested using judgment tasks where children are verbally questioned about whether they think an obstacle is passable or not; or where they are asked to choose a preferred path through an environment. These visually guided “passability” judgments depend on the perceived skill required to cross an obstacle, and the perceived size of the obstacle relative to one’s own body dimensions (Adolph 1995; Kingsnorth and Schmuckler 2000; Schmuckler 1996). Visual information is particularly useful in determining obstacle size, and by mid-childhood this body-referenced size information is very tightly coupled to passability judgments (Heinrichs 1994; Pufall and Dunbar 1992). These judgments become more refined during early childhood: For example, older toddlers judge better than younger toddlers whether a barrier can be stepped over (Schmuckler 1996) or a gap crossed (Zwart *et al.* 2005).

Haptic information can also contribute to locomotor judgments. For example, Adolph (1995) compared children’s perceptions of which slopes they could walk on with their actual abilities. 14-month-olds made fewer attempts to descend slopes as they became steeper, but nonetheless overestimated their abilities. Crucially, these

infants explored the slopes before they descended. The exploration was structured, consisting of a short look at the slope, followed, if necessary, by a long look, then exploring the slope by touch, and then trying alternative methods of descent such as sliding down (Adolph 1997). Exploration was used to inform locomotor choices, with most exploration at those slopes which were neither obviously easy to descend nor obviously impossible, but required careful consideration. Thus haptic information was added to visual information in locomotor decision-making at this young age. Sensory exploration persists at older ages. In one task, children of 4.5 years were asked to judge whether they could stand upright on a ramp (Klevberg and Anderson 2002). Their judgements were compared with their actual competence. They could explore the ramp using either vision or touch (for touch, they felt the ramp with a wooden pole). Children overestimated their ability to stand on the slopes. Like adults, they judged more accurately in the visual exploration condition than in the haptic exploration condition. Thus both visual and haptic information can be used for exploration of the locomotor environment, though further work is needed to explore the balance of these inputs in more detail.

Online feedback can help to correct and refine movements which are already underway. In locomotion, a wide range of sensory inputs can potentially provide feedback including visual, proprioceptive, vestibular and tactile inputs. Using feedback to guide actions may be particularly important in childhood. This is apparent in a stair descent task. With vision available during the whole stepping movement, three-year-olds are skilled at using visual information about stair size to scale their movements to the size of step they are descending. However, this ability is significantly impaired when visual feedback is removed during the step down (Cowie *et al.* 2010). This suggests a need for visual feedback at 3 years, which disappears by 4

years. In a more complicated obstacle avoidance task that required careful foot placement as well as movement scaling, degrading vision impaired performance even for 7-year-old children (Berard and Vallis 2006). Thus, some existing data suggests that visual feedback may be crucial for complex aspects of walking throughout childhood. A recent eye-tracking study with young children (Franchak and Adolph 2010) confirms that during obstacle navigation children make more fixations than adults. More work is needed to establish the dynamics of sensory inputs and motor outputs during locomotion. Furthermore, it is clear that the extent of reliance on visual feedback depends on task complexity, and one of the challenges for locomotor research is to formulate general developmental principles regarding the use of sensory information in locomotor tasks.

2.3 Multisensory development of balance and locomotion: conclusions

Although balance and locomotion have here been reviewed separately, in fact these two skills are highly interdependent. While balance skills allow the child to walk safely, locomotion also refines the control of balance. Infants who can sit upright respond better to balance perturbations than those who cannot (Woollacott *et al.* 1987), and infants with crawling or locomotor experience sway less than those without (Barela *et al.* 1999). Locomotor experience can also alter the sensory control of balance: For example, experienced walkers are more responsive to specific aspects of sensory stimuli, such as peripheral optic flow (Higgins *et al.* 1996).

We have reviewed a range of evidence which suggests important transitions from an early reliance on vision for balance and locomotion, to a later pattern where information from across the visual, proprioceptive, and vestibular systems is responded to in a more even way. What precisely do we mean by “reliance”, and what

are the mechanisms underlying such change? One model of multisensory processing leading to action is that during development estimates from one, predominant, sense, are simply acted upon in disregard of estimates from the other responses. It is easy to imagine infants' responses to the visual swinging room stimulus in terms of this sort of mechanism. This can be contrasted with a second type of model in which a central integrator collates and weights information from the independent senses to produce a final multisensory estimate, which can then be acted upon (Clark and Yuille 1990; Ernst 2005; Körding and Wolpert 2006). In the concluding section of this chapter (**Section 5**), we will discuss models of information integration in more detail, argue that they provide a useful framework for future lines of investigation, and highlight the experimental manipulations that still need to be carried out in order to evaluate them.

3. Development of multisensory orientation and navigation

Balance and locomotion provide a basis for spatial behaviour. To be adaptive, spatial behaviour must be directed towards (or away from) significant objects and locations in the environment. In this section we consider the development of the ability to orient and navigate to significant objects and locations. Information about objects and locations commonly comes from multiple senses (*e.g.*, vision, audition, touch), which must be combined appropriately. Information about one's own movement in space also comes from multiple senses (*e.g.*, vision, audition, proprioception and the vestibular system). Many spatial tasks, such as picking up an object or crossing a road, require an immediate response to environmental stimuli but no lasting record of them. Other spatial tasks, such as finding the keys or finding the way home, also require

memory. In these tasks, multisensory spatial information must be stored in a form that is useful for later retrieval.

3.1. Multisensory orienting

Orienting the eyes and head towards salient nearby stimuli is a basic spatial behaviour evident from birth. Newborns orient to visual patterns (especially faces), but also to auditory and tactile stimuli (Clifton *et al.* 1981; Fantz 1963; Moreau *et al.* 1978; Tan and Tan 1999; Wertheimer 1961). Early visual orienting is driven by the retinotectal pathway to the superior colliculus in the midbrain, which transmits sensory information for eye and head movements (Bronson 1974). This subcortical system enables orienting to salient single targets, but not fine discrimination or target selection. Cortical processing of visual stimuli, enabling increasingly fine discriminations (*e.g.*, of orientation, motion, or binocular disparity), develops in the first months of life (Atkinson 2002). Selective attention, enabling flexible selection of targets (for example, disengagement from a central target in order to fixate a peripheral target) develops at 3-4 months (Atkinson *et al.* 1992), and represents further cortical control over orienting behaviour (Braddick *et al.* 1992).

Orienting responses alert infants to potentially interesting or hazardous objects, and enable them to collect additional sensory information about them. Since the same objects can be signalled by information from multiple modalities (*e.g.*, vision, audition, touch), orienting responses need to be driven by multiple sensory inputs. In addition, as multisensory inputs are unlikely to come from a similar spatial location at the same time purely by chance (see Kording *et al.* 2007), such stimuli are likely to represent significant objects in the environment. The superior colliculus supports multisensory orienting by integrating spatially localized visual, auditory, and

somatosensory inputs within a common reference frame (see **Chapter 11** by Laurienti and Hugenschmidt and **Chapter 14** by Wallace *et al.*). A proportion of multisensory neurons in the cat superior colliculus have “superadditive” properties: They fire to auditory-only and visual-only stimuli localized at the same point in space, but the firing rate for visual-and-auditory stimuli is greater than for the sum of the two single stimuli (Meredith and Stein 1983; Meredith and Stein 1986; Wallace *et al.* 1996). This property indicates that these neurons have a dedicated role in the processing of stimuli providing both auditory and visual information at the same time. This multisensory neural organization is not present in newborn cats or monkeys (Wallace and Stein 1997, 2001) but develops in a manner dependent on sensory experience (**Chapter 14** by Wallace *et al.*).

Spatial co-location of auditory and visual events is detected by infants at least by 6 months of age (Lawson 1980). To investigate the early development of multisensory integration for spatial orienting, Neil *et al.* (2006) measured the latencies of 1- to 10-month-olds’ head and eye movements towards auditory-only, visual-only, or auditory and visual targets located left or right of the midline. In theory, having two stimuli available at once can enable a purely “statistical facilitation” of reaction times, since there are two parallel opportunities to respond (Miller 1982; Raab 1962). Given parallel processing but no interaction between cues, observers responding to whichever cue is processed first on any given trial will show a predictable decrease in mean reaction time relative to single cues. This purely “statistical” improvement is described by the “race model”: (Miller 1982; Raab 1962; see also Otto and Mamassian 2010), in which the two cues being processed in parallel are in a “race” to initiate a response. To show evidence for multisensory interaction, it is therefore necessary to show speed advantages for two cues *vs.* one that are greater than those predicted by the

race model. Neil and colleagues (2006) found latency gains given two cues rather than one at all ages; however, it was only at 8 to 10 months that these exceeded the statistical facilitation predicted by the race model. This indicates that mechanisms for multisensory facilitation of audiovisual orienting emerge late in the first year of life in humans, consistent with the experience-dependent postnatal development that has been reported in the superior colliculus in monkeys and cats (Wallace and Stein 1997, 2001; see **Chapter 14** by Wallace *et al.*).

Interestingly, when participants did not use eye or head movements to localize audiovisual stimuli, but responded to them by pressing a button as quickly as possible (a “detection” task), adult-like multisensory improvements in latency were not evident until after 7 years (Barutchu *et al.* 2009; Barutchu *et al.* 2010). It may be that these tasks do not tap into the early-developing subcortically driven reflexive orienting system, but require cortical evidence integration and selection for action (Romo *et al.* 2004), which may develop later. To investigate this possibility, the latest research has started to compare manual and eye-movement responses to the same audio-visual stimuli directly (Nardini *et al.* in press).

3.2. Orienting and reaching while taking own movement into account

To localize targets that are perceptually available at the time of test, an egocentric coordinate system is sufficient, and no memory is needed. However, significant objects in the environment are not continually perceptually available, and may become hidden from view or silent to the observer. This is particularly the case with mobile observers, who can change their perspective on spatial layouts from one moment to the next. For infants beginning to crawl and walk independently, a crucial challenge is to integrate multisensory information into spatial representations that are useful for

relocating objects after a change of position. Infants who are passively carried must likewise take their movements into account in order to keep track of nearby objects' locations¹.

After movement, a static object initially localized on the observer's left can take up a new position in egocentric space, such as behind or to the right. The original egocentric representation of the object's location is then no longer useful for retrieving it. This problem can be overcome in two ways: By updating objects' positions in egocentric coordinates while moving ("spatial updating"), or by using external landmarks such as the walls of the room to encode and retrieve locations. For spatial updating, the observer's own movement, ("self-motion"), needs to be taken into account. In human adults, both self-motion and landmarks play major roles in spatial orientation and navigation (for reviews see Burgess 2006; Wang and Spelke 2002). Within the broad category of "landmarks" key questions concern the extent to which these help to organize space into a geocentric "cognitive map", and the extent to which they are used for simpler strategies such as recognition of familiar views (Burgess 2006; Wang and Spelke 2002). For humans, useful landmarks are overwhelmingly visual². Information about self-motion, however, comes from many sensory sources: from vision, *via* optic flow (J.J. Gibson 1979; see **Section 2** above), as well as from vestibular, kinesthetic, and proprioceptive inputs (Howard and Templeton 1966; MacNeilage *et al.* 2007; Zupan, *et al.* 2002).

Until recently, little was known about the neural mechanisms underlying integration of multiple self-motion inputs for spatial behaviour. Important advances have been in showing how macaque MST neurons integrate visual and vestibular information to compute the animal's direction of movement (Gu *et al.* 2008; Morgan *et al.* 2008). Self-motion information must further be integrated with visual landmarks.

A range of cell types in the mammalian medial temporal lobe (“head direction cells”, “grid cells”, and hippocampal “place cells”) encode both self-motion and landmark information and are likely to be the basis for their integration (for reviews see Burgess 2008; McNaughton *et al.* 2006; Moser *et al.* 2008; Taube 2007).

The earliest situations in which human infants might take their own motion into account to localize objects are before independent movement, when carried passively. Infants’ spatial orienting in these situations has been investigated in studies using “peekaboo” tasks. In a study by Acredolo (1978), 6- to 16- month-olds sat in a parent’s lap at a table inside a square enclosure with windows to the left and right. In a training phase, infants learned that whenever a buzzer sounded, an experimenter appeared at one of the windows. This was always the same window for each child. Once the infant had learnt to orient to the correct window when the buzzer sounded, the testing stage began. The parent and infant moved to the opposite side of the table, a manipulation that swapped the egocentric positions of the “left” and “right” windows. When the buzzer sounded, the experimenters recorded whether the infant looked to the correct window, showing that they had correctly processed their change of position. With no distinctive landmarks distinguishing the windows, solving the task depended on the use of self-motion information, *e.g.*, from optic flow and the vestibular system. Infants up to 11 months old failed to use such information and oriented to the incorrect window.

Other studies have confirmed the poor abilities of infants in the first year to update their direction of orienting using only self-motion information (Acredolo and Evans 1980; Keating *et al.* 1986; McKenzie *et al.* 1984; Rieser 1979). However, when direct landmarks are added to distinguish between locations, infants in the first year orient correctly (*e.g.*, at 6 months in Rieser 1979, and at 8-11 months in Acredolo and

Evans 1980; Keating *et al.* 1986, Lew *et al.* 2000 and McKenzie *et al.* 1984). Similarly, when searching for objects hidden in the left or right container on a table-top, infants in the first year moved to the opposite side of the table tend not to take their own movement into account unless they are given useful landmarks in the form of colour cues (J.G. Bremner 1978; J.G. Bremner and Bryant 1977).

These results suggest that in order to maintain the locations of nearby objects following their own movement, infants in the first year found added visual landmarks significantly more useful than self-motion information alone. As stated above, self-motion information comes from a number of sensory inputs. These may mature at different rates, and interactions between them to guide self-motion perception may also mature unevenly, as is the case with balance (see **Section 2**, above). In “peekaboo” and reaching tasks, infants have optic flow and vestibular cues to changes of position. Older infants and children carrying out the movement themselves can also use kinesthetic and motor efference information about the movement of their body. Children perform better after moving actively than after being carried (Acredolo *et al.* 1984), and better when walking around to the opposite viewpoint than when the opposite viewpoint is presented by rotating the spatial layout (J.G. Bremner 1978; J.G. Bremner and Bryant 1977; Schmuckler and Tsang 1997). This indicates that kinesthetic and motor-efference information is useful. Performance is also better in the light than in the dark, consistent with use of optic flow (Schmuckler and Tsang-Tong 2000). There is however as yet little direct evidence for whether, when, and how infants integrate these multiple potential information sources to orient themselves in space. J.G. Bremner *et al.* (1999) separated the contributions of optic flow and vestibular cues to 6- to 12-month olds’ abilities to orient correctly to a target after a change of position. Infants were seated in a rotatable cylindrical surround, which

allowed manipulation of visual and vestibular information separately and in conflicting combinations. The results showed a U-shaped developmental pattern in which 6-month-olds, 12-month-olds, and young adults responded on the basis of optic flow information, whereas 9-month-olds responded predominantly on the basis of vestibular information. This indicates that children's reliance on visual *vs.* vestibular information for locating targets undergoes marked changes in the first year.

3.3. Navigation and spatial recall

The natural extension of early orienting and reaching responses towards nearby objects is to flexible navigation and spatial recall in extended environments. This depends on observers being able to encode locations using frames of reference that will be useful for their later retrieval, and to bind individual objects (“what”) to their locations (“where”). As described above, mature navigation and recall depend critically both on visual information about landmarks and multisensory information about self-motion.

Spatial studies with children of walking age have typically used search tasks in which the child sees a toy hidden, and must then find it given a specific set of cues or after a specific manipulation. Evidence for the individual development of landmark-based and self-motion based spatial recall has come from tasks that separate these information sources completely. Following spatial tasks devised for rodents by Cheng and Gallistel (Cheng 1986; Gallistel 1990), Hermer and Spelke (1994, 1996) used “disorientation” to eliminate self-motion information and so test spatial recall based only on visual landmarks. In their task, 18- to 24- month-olds saw a toy hidden in one of four identical containers in the four corners of a rectangular room. Useful landmarks were the ‘geometry’ of the room (*i.e.*, whether the target box had a longer

wall on its left or its right), and in some conditions, different wall colours. If the child was simply turned to face a random direction and then allowed to search, they could relocate the toy using not only these visual landmarks but also an egocentric representation. Such a representation might be an initial vector (*e.g.*, “on my left”) that has been updated with self-motion to take the child’s recent turn into account. To eliminate this information source, children were disoriented by repeated turning with eyes closed before being allowed to search. The resulting searches therefore reflected only the accuracy of visual landmarks, and not of egocentric representations updated with self-motion.

A large body of research using this technique has demonstrated that children as young as 18 to 24 months can recall locations using only indirect visual landmarks, although their abilities to use some kinds of indirect landmark (*e.g.*, “geometry”, or the shape of the enclosure layout) can be markedly better than others (Huttenlocher and Lourenco 2007; Learmonth *et al.* 2002, 2008; Lee *et al.* 2006; Lee and Spelke 2008; Nardini *et al.* 2009; Newcombe *et al.* 2010; for reviews see Cheng and Newcombe 2005; Twyman and Newcombe 2010).

The converse manipulation used to test self-motion alone, without use of visual landmarks, is blindfolding participants. Strictly, this a test for use of non-visual (*e.g.*, vestibular) self-motion cues only, as removing vision also removes the optic flow cue to self-motion³. A typical non-visual “self-motion-only” spatial task is one in which the participant is walked along the two lines of an “L” and then asked to return directly to the origin, *i.e.*, to complete the triangle (Foo *et al.* 2005; Loomis *et al.* 1993). Such a task depends on keeping track of one’s own directions and angles of movement since leaving the origin. There have been relatively few studies quantifying development of self-motion-only navigation. Rider and Rieser (1988) found that 2-year-olds could

localize targets after blindfolded walking along routes with two 90° turns, as could 4-year-olds, who were more accurate. In another study, four-year-olds' errors, like adults', increased with numbers of turns and numbers of targets (Rieser and Rider 1991). While 4-year-olds were inaccurate compared with adults, they still performed better than chance given up to three turns and five targets. These results suggest that like the landmark-only based localization of targets, self-motion-only based localization emerges quite early in development. However, developmental trajectories for different self-motion inputs (*e.g.*, vestibular *vs.* kinesthetic), or their integration, have not yet been studied.

The usual case, of course, is one in which both landmarks and self-motion are available. For example, in order to relocate an object that we have recently put down elsewhere in the room we can use visual landmarks, as well as a self-motion-updated egocentric estimate of where the object now is relative to us. A key question is how these systems interact to guide spatial behaviour. For mammals, including humans, landmarks are usually more useful and exert stronger control over behaviour (Etienne *et al.* 1996; Foo *et al.* 2005). Landmark and self-motion systems can be seen as complementary, in the sense that self-motion can help when landmarks are not available. On this model, self-motion is a “back-up” system for landmarks. An alternative model is one in which self-motion and landmarks are integrated to improve accuracy. That is, neither system provides a fully reliable guide to location, but by integrating them estimates of location can be made more reliable. This second view is in line with Bayesian models of multisensory and spatial behaviour (Cheng *et al.* 2007; Clark and Yuille 1990; Ernst 2005; Körding and Wolpert 2006; see below and **Section 5**).

A number of studies have examined the development of spatial recall in situations allowing use of both self-motion and landmarks. In studies by Huttenlocher, Newcombe and colleagues (Huttenlocher *et al.* 1994; Newcombe *et al.* 1998), children searched for toys after seeing them buried in a long sandbox. The 1994 study established that 16- to 24-month olds used the edges and overall shape of the sandbox as visual “landmarks” when retrieving toys while remaining on the same side of the box. In the 1998 study, 16- to 36-month-olds walked around the box to retrieve toys from the opposite side. From the age of 22 months, having additional distant landmarks in the room visible improved the accuracy of retrieval from the opposite side. The role of these cues may have been to provide distant landmarks situating the box and locations in a wider reference frame, and to improve spatial updating with self-motion by highlighting the change in perspective brought about by walking to the opposite side. In either case, these results are consistent with use of both visual landmarks and multisensory self-motion inputs to encode spatial locations in the first years of life.

Simons and Wang (1998; Wang and Simons 1999) showed that human adults’ recall for spatial layouts from new viewpoints is more accurate when they walk to the new viewpoint than when they stay in one place while the layout is rotated. With rotation of the layout, use of visual landmarks alone allows adult observers to understand the change of perspective and to relocate objects with a certain level of accuracy. However, this accuracy is enhanced when subjects walk to the new location, meaning that self-motion information is also available (see also Burgess *et al.* 2004).

To study the development of coding based on both visual landmarks and self-motion, Nardini *et al.* (2006) tested 3- to 6-year olds’ recall for the location of a toy hidden under an array of cups surrounded by small local landmarks. Vision was

always available. However, on some trials, recall took place from the same viewpoint, while on others recall was from a different viewpoint. Viewpoint changes were produced either by the child walking (so gaining self-motion information about the viewpoint change), or by rotation of the array (gaining no self-motion information). At all ages recall was most accurate without any viewpoint change. With viewpoint changes produced by walking, the youngest children (3-year-olds) were above chance, and quite accurate, at relocating objects. However, with viewpoint changes produced by array rotation, only 5- and 6-year-olds retrieved objects at rates above chance. This indicates that self-motion information is a major component of early spatial competence, and can dominate over visual landmarks: Without useful self-motion information, and so using only visual landmarks, 3- and 4-year olds could not correctly process the viewpoint change. Note that when disoriented and so unable to use self-motion, children from 18-24 months are competent at using some kinds of visual landmarks to recall locations (Hermer and Spelke 1994, 1996). The present case is more complex in that instead of being eliminated as by disorientation, when the array was rotated self-motion information remained available, but indicated the wrong location. This study therefore set up a conflict between visual landmarks and self-motion, and found that before 5 years children preferred to rely on self-motion, even when it was inappropriate for the task.

In a subsequent study, Nardini *et al.* (2008) used a different method to measure how self-motion and landmarks interact for spatial recall. The cues were not placed in conflict, as by array rotation manipulations, but were separated completely in “landmark-only” and “self-motion-only” conditions. This enabled a more formal test for their integration, and comparison with a Bayesian “ideal observer” model (Cheng *et al.* 2007; Clark and Yuille 1990; Ernst 2005; Körding and Wolpert 2006). As in

earlier studies, “landmark only” performance was measured using disorientation, and “self-motion only” performance was measured using walking in darkness. However, these manipulations were now carried out within the same spatial task, and were compared with a combined “self-motion and landmarks” condition within the same participants.

Four- to 8-year-olds were tested in a dark room with distant glowing landmarks, and a set of glowing objects on the floor (**Fig. 6.3A**). The task was to pick up the objects on the floor in a sequence, and then to return the first object directly to its original place after a short delay. In “visual landmarks only” and “(non-visual) self-motion only” conditions, participants had to return the object after disorientation and in darkness respectively. A “self-motion plus landmarks” condition tested the normal case in which participants were not disoriented and landmarks remained available. Bayesian integration of cues predicts greater accuracy (reduced variance) given both cues together than either single cue alone. In a “conflict” condition the landmarks were rotated by a small amount before participants responded. They did not detect this conflict, but it provided information about the degree to which participants followed one or the other of the two information sources.

--Insert Figure 6.3 about here--

Adults were more accurate in their spatial estimates given both self-motion and landmarks, in line with optimal (ideal observer model) performance. Given two cues rather than one, adults’ searches were on average closer to the target (**Fig. 6.3B**) and less variable⁴ (**Fig. 6.3C**). By contrast, 4- to 5-year-olds and 7- to 8-year-olds did not perform better given two cues together than the best single cue (**Fig. 6.3B, C**).

Modelling of responses on the “conflict” condition indicated that while children can use both self-motion and landmarks to navigate, they did not integrate these but followed one or the other on any trial. Thus, while even very young children use both self-motion and landmarks for spatial coding, they seem not to integrate these to improve accuracy until after 8 years of age. Proposed neural substrates for integration of self-motion and landmarks for spatial tasks are head place cells, direction cells, and grid cells in the hippocampus and medial temporal lobe (for reviews, see Burgess 2008; McNaughton *et al.* 2006; Moser *et al.* 2008; Taube 2007). Late development of spatial information may be reflected in development of these medial temporal networks. Recent studies with rodents have found these cell types to be functional very early in life (Langston *et al.* 2010; Wills *et al.* 2010), although the development of their abilities to integrate multisensory information is still to be investigated.

The late development of multisensory integration for reducing uncertainty in spatial tasks parallels that recently reported for visual-tactile judgments of size and shape (Gori *et al.* 2008) and for multiple visual depth cues (Nardini *et al.* 2010). It is possible that while mature sensory systems are optimised for reducing uncertainty, developing sensory systems are optimised for other goals. One benefit of not integrating multisensory cues could be that keeping cues separate makes it possible to detect conflicts between them. These conflicts may provide the error signals needed to learn correspondences between cues, and to recalibrate them while the body is growing (Gori *et al.* 2010).

4. Summary

We have reviewed the development of sensory integration for the skills underpinning human spatial behaviour: balance, locomotion, spatial orientation, and navigation. Even very young children are capable of using sensory information in order to control balance and locomotion. Visual information seems particularly heavily weighted in infancy and early childhood. Around 5 to 6 years a period of change begins, where visual information is gradually down-weighted in favour of somatosensory and vestibular inputs. However, on the available evidence, balance and locomotion are not coupled in an adult-like fashion to either somatosensory or visual information until adolescence.

Early spatial orienting behaviours show multisensory facilitation late in the first year, consistent with experience-dependent postnatal development of the superior colliculus. Sensory integration for more complex orientation and navigation tasks including localising objects again after own movement shows a much more extended developmental trajectory. Both self-motion information and landmarks are used for spatial orientation and navigation from an early age, however they may not be integrated in an adult-like fashion until after 8 years of age. Neural bases for these tasks are increasingly becoming understood in animal models, and mathematical models are increasingly allowing sensory integration during development to be precisely quantified. A major challenge for the future is to account for developmental change by linking these mathematical and neural levels of analysis.

5. Bayesian models

We have proposed at several points in this chapter that Bayesian models of information integration can provide a useful framework for understanding developmental balance, locomotion and navigation phenomena. Here we briefly describe the models and the prospects for further tests of their application to multisensory developmental phenomena in the future.

Bayesian models address the problem that individual sensory estimates are inevitably variable (uncertain) because of random noise. “Noise” is evident in an auditory environment with background noise, or a murky visual environment; however, even in ideal environmental conditions, all sensory systems contain some variability (uncertainty) due to their own limited resolution, and to noisy transmission of information by neurons. Bayesian models provide a rule by which the multiple, noisy, sensory estimates we usually have available in parallel can be combined to provide a single estimate that minimises noise or uncertainty (Cheng *et al.* 2007; Clark and Yuille 1990; Ernst 2005; Körding and Wolpert 2006).

The rule for combining estimates to reduce uncertainty is simple: If multiple sensory estimates are available (*e.g.*, visual and haptic cues to object size), and the noise in each of these is independent, then taking a *weighted average* of the estimates will produce a final estimate that is less variable (more reliable) than the component estimates. The optimal weighting is one in which the different estimates are weighted in proportion to their reliabilities. A cue that is three times more variable than another is therefore given three times less weight. Recent multisensory studies with adults have shown optimal multisensory integration in many situations (*e.g.*, vision and touch, Ernst and Banks 2002; vision and audition, Alais and Burr 2004; visual and vestibular cues to direction of heading, Fetsch *et al.* 2009; reviews: Ernst 2005; Körding and Wolpert 2006).

These findings provide an important new perspective on human multisensory processing in demonstrating that in adults at least, multisensory integration is very flexible. Adults are excellent at dynamically “reweighting” their reliance on different information sources when these change in reliability. Thus, although vision may usually dominate for a particular task, if visual information becomes uncertain (*e.g.*, at night, or in fog) it will be given less weighting relative to the other available information (Alais and Burr 2004). The conclusion from this and other studies is that phenomena such as “visual dominance” may be explained simply by the differing reliabilities of the senses for particular tasks (Ernst 2005; Körding and Wolpert 2006). Task-specific explanations for cue weighting: *e.g.*, that vision dominates over audition for spatial localization (Pick *et al.* 1969) - can then be subsumed by a single, more general explanation: vision and audition (and other sensory inputs) are weighted according to their reliabilities; Alais and Burr 2004).

We have described a range of developmental phenomena in which visual dominance changes with age. For example, balance is much more influenced by vision in young children than it is in older children or adults (Godoi and Barela 2008; Shumway-Cook and Woollacott 1985; Wann *et al.* 1998; Woollacott *et al.* 1987). We can state two possible kinds of Bayesian explanation for this developmental pattern. First, **Possibility 1: children and adults integrate multisensory information in the same Bayesian / “optimal” manner.** In this scenario, developmental changes in “dominance” might simply reflect developmental changes in the reliabilities of the underlying estimates. If the development of different senses were uneven (*e.g.*, if visual information for balance was accurate at an earlier age than vestibular information), then different ages would show different weightings even though they were following the same integration rules. A prediction from this account is that adults

whose cue reliabilities were manipulated (*e.g.*, by selectively adding noise) to be the same as children's would show the same behaviour as children.

The issue of dynamic sensory reweighting in children's balance control was first raised by Forssberg and Nashner (1982), and several studies since have investigated the swinging room experiment from this perspective, changing the distance between the swinging walls and the observer to try and detect sensory reweighting as the far walls become a less reliable source of information about relative motion (Dijkstra *et al.* 1994; Godoi and Barela 2008). Studies have also recorded developmental changes in weighting of multisensory information for posture control in response to differing amplitudes of visual *vs.* somatosensory perturbations (Bair *et al.* 2007). However, to be able to test whether patterns of reweighting in either children or adults are in line with Bayesian predictions, studies will need to measure the *sensory reliabilities* of visual and other cues to balance, which remains challenging (see below).

The alternative is **Possibility 2: children and adults do not integrate multisensory information in the same Bayesian / “optimal” manner.** For example, adults might take a weighted average of estimates in proportion to their reliabilities, while children might do something else. Children could rely on a single estimate even when other reliable estimates are available, or, they could integrate estimates using a sub-optimal weighting, or they could be less effective than adults in excluding estimates that are highly discrepant with others from the integration process⁵.

Most of the studies that have been reviewed cannot separate these two accounts, as changes with age in relative reliance on different cues are consistent with both. Possibility 1 – that children and adults process information in the same way – provides the simplest account in that it needs to posit fewer kinds of developmental

changes. This account therefore should not be ruled out for specific tasks until the relevant experimental manipulations have been tested. Interestingly, in the small number of studies that have examined the development of Bayesian integration explicitly (Gori *et al.* 2008; Nardini *et al.* 2008; Nardini *et al.* 2010), children were shown *not* to integrate estimates in an adult-like way until after 8 years – *i.e.*, Possibility 1 could be rejected. These studies used visual, manual and locomotor tasks involving spatial or psychophysical decisions. Whether the same would be true for more elementary sensory-motor behaviours such as balance is a major question for future studies. A challenge for developmental studies is the time-consuming nature of testing Bayesian models of multisensory integration, since they require measurement of response variability in both single-cue and combined-cue conditions. One way to address this is use of psychophysical staircase procedures (*e.g.*, Kaernbach 1991; Kontsevich and Tyler 1999) to obtain more rapid estimates of variability (Nardini *et al.* 2010). A second challenge is measuring perceptual variability for elementary sensory-motor behaviours such as balance that lead to postural changes but do not lend themselves to explicit judgments. For this, new approaches need to be developed for inferring variability from spontaneous behaviours. This is challenging but possible, as a recent study has shown by measuring integration of depth cues using only spontaneous eye movements (Wismeijer *et al.* 2010).

To sum up, many developmental changes in use of multiple cues for balance, locomotion and navigation in childhood could be explained within a Bayesian framework. However, to assess whether developmental changes correspond either to adult-like integration with a different inputs in terms of cue reliabilities, or non-adult like integration or lack of integration, more detailed studies need to be carried out quantifying the variability of the underlying estimates. The few studies so far that have

tested this framework with children suggest that they do not integrate estimates in an adult like manner until after 8 years, across senses for spatial localization or object perception (Gori *et al.* 2008; Nardini *et al.* 2008), or within vision for 3D shape discrimination (Nardini *et al.* 2010).

5.1. Other models

We have reviewed development of the sensory processes underlying adaptive spatial behaviour. While children's sensory and motor systems are immature, they are also in some senses optimized for the ecology of their environments. For example, young infants do not need high visual acuity or accurate spatial localization. Bayesian models stress optimization for accuracy, in terms of the reduction of sensory uncertainty. However, maximal accuracy is not the most important goal for many spatial tasks that infants and children face. For developing sensory-motor systems there may be other goals more important than maximizing accuracy, such as responding rapidly (Barutcu *et al.* 2009; Neil *et al.* 2006), or detecting inter-sensory conflicts (Gori *et al.* 2010; Nardini *et al.* 2010). Therefore many other kinds of model remain to be developed, in which "optimality" is quantified based on different goals or properties. It may be that these models will provide the best description of how developing perceptual and motor systems are optimized for spatial behaviour.

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FOOTNOTES

1. A related problem is keeping track of own limb positions in order to enable their accurate localization, and to support accurate reaching towards objects (**Chapter 5** by A.J. Bremner *et al.* and **Chapter 13** by Röder *et al.*; A.J. Bremner *et al.* 2008a; 2008b; Pagel *et al.* 2009).

2. If landmarks do play a role in building up a “cognitive map” of space, an interesting question is how and whether blind humans do this (Klatzky *et al.* 1990; Loomis *et al.* 1993).

3. In a study with adults, Riecke *et al.* (2002) separated the dual roles of vision in providing visual landmarks and optic flow by having subjects navigate in virtual reality through a field of visual ‘blobs’ that provided texture for optic flow but could not be used as landmarks.

4. The major predicted benefit for integration of cues is a reduction in the *variance* of responses – see **Section 5**.

5. The simple rule to integrate *all* available estimates is inappropriate for situations in which one estimate differs drastically from the others. “Robust cue integration” is an extension to the Bayesian integration framework stating that since large outliers are highly unlikely to be due to normal sensory noise, they should be presumed to be erroneous and excluded from integration with other estimates (Knill 2007; Kording *et al.* 2007; Landy *et al.* 1995). “Robust cue integration” would give observers in the

swinging room a basis for disregarding visual information when it is highly discrepant with vestibular and proprioceptive information. The crucial point to note in comparing children and adults is that whether or not estimates can be detected as “highly discrepant” depends not only on the average difference between them, but also on their variabilities. Thus, given children and adults subjected to the same experimental manipulation, if adults’ estimates of own posture (via all senses) are much less variable than children’s, then adults might have a basis for detecting that the visual estimate is discrepant compared with the others, whereas children might not. In this situation, if both age groups were following “robust cue integration” with the same integration rules, adults would reject vision but children would not. To show that adults and children really differ in integration behaviour it is necessary to exclude this possibility – for example, by showing that even when noise is added to adults’ estimates in order to bring them to children’s level, they still behave differently.

FIGURE CAPTIONS

Fig. 6.1. The swinging room technique. **(a)** The participant stands in a room with a stationary floor but moving walls. **(b)** An optic flow expansion pattern created by walls moving toward the participant. The same pattern would be produced by the observer swaying forward.

Fig. 6.2. Measuring multisensory contributions to balance. While participants attempt to stand still on a platform, visual information can be removed by closing the eyes. Ankle joint proprioception can be made unreliable by rotating the platform to maintain the ankle at a fixed angle. This creates four sensory conditions **a-d** during which sway was measured (Shumway-Cook and Woollacott 1985).

Fig. 6.3. **(A)** Layout for the Nardini et al. (2008) spatial task. **(B)** Mean Root Mean Square Error (RMSE) of responses under conditions providing SM (self-motion), LM (landmarks), or SM+LM (both kinds of information). This measure reflects distances between each search and the correct location. **(B)** Standard deviation (SD) of responses. This measure reflects the variability (dispersion) of searches. Bayesian integration of cues predicts reduced variance (and hence also reduced SD, which is the square root of the variance), given multiple cues.

Figure 6.1

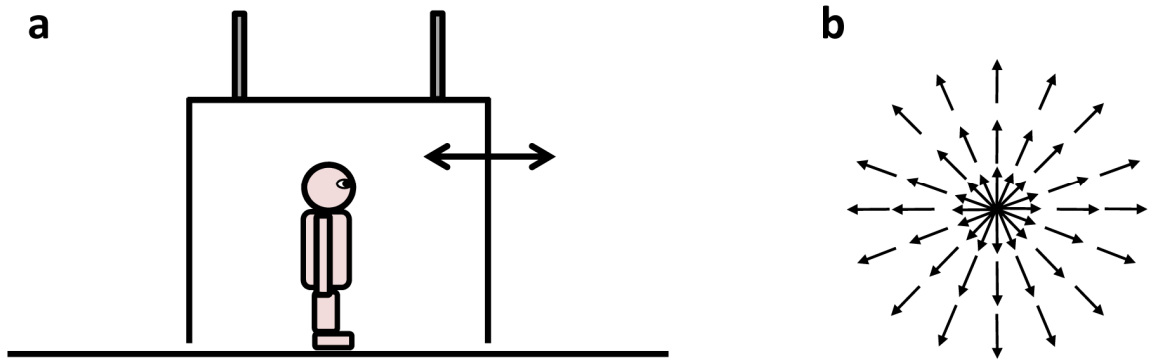


Figure 6.2

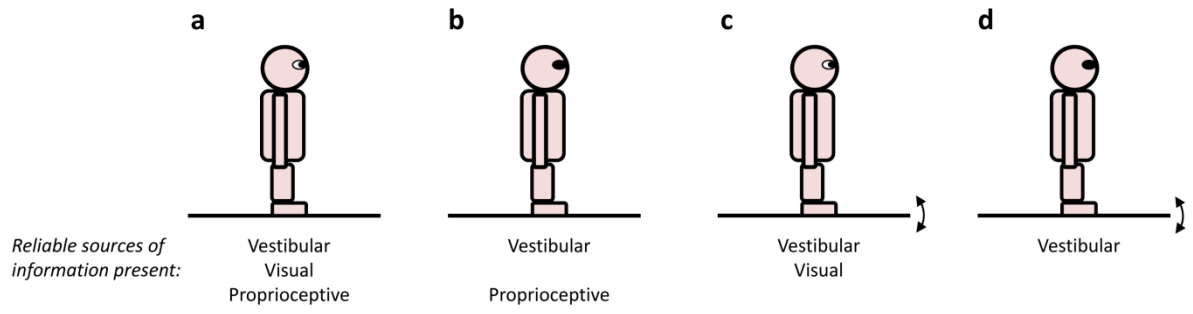


Figure 6.3

