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The contribution of visual and vestibular information to spatial orientation by 6- to 14-month-old infants and adults

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Abstract

Although there is much research on infants' ability to orient in space, little is known regarding the information they use to do so. This research uses a rotating room to evaluate the relative contribution of visual and vestibular information to location of a target following bodily rotation. Adults responded precisely on the basis of visual flow information. Seven-month-olds responded mostly on the basis of visual flow, whereas nine-month-olds responded mostly on the basis of vestibular information, and 12-month-olds responded mostly on the basis of visual information. Unlike adults, infants of all ages showed partial influence by both modalities. Additionally, 7-month-olds were capable of using vestibular information when there was no visual information for movement or stability, and 9-month-olds still relied on vestibular information when visual information was enhanced. These results are discussed in the context of neuroscientific evidence regarding visual-vestibular interaction, and in relation to possible changes in reliance on visual and vestibular information following acquisition of locomotion.

The contribution of visual and vestibular information to spatial orientation by 6- to 12-month-old infants and adults

When adults move around the world, they are adept at maintaining a sense of their position in space despite extensive bodily displacements and reorientations. It is easy to overlook this process, given its frequently effortless nature. But it is clearly a fundamental component of spatial processing and, in addition to reaching an understanding of its basis in adults, it is important to understand its developmental origins from infancy onwards.

Typically, research on infant spatial orientation investigates infants' ability to relocate a target following some form of bodily movement and/or reorientation. Several researchers have investigated the conditions under which infants relocate a fixed target after a bodily rotation. One method (Cornell & Heth, 1979; Keating, McKenzie, & Day, 1986; McKenzie, Day, & Ihsen, 1984; Rieser, 1979) measures infants' anticipation of an event at a constant position; infants are trained to look towards a fixed locus and are then rotated to a new direction of facing, and direction of anticipatory looking is measured. The picture to emerge from this and similar methods is that between four and eight months of age infants show an increasing ability to take account of bodily rotation (Keating et al., 1986; McKenzie et al., 1984; Meuwissen & McKenzie, 1987; Rieser, 1979).

One important gap in our knowledge of the processes of infant spatial orientation concerns the relative contribution of visual and vestibular[1] information. Although there is evidence regarding visual-vestibular interaction in early infancy (Rosander & von Hofsten, 2000), this concerns the effects on gaze adjustment during stimulation and not spatial orientation as such. On the one hand, evidence regarding the importance of landmarks in spatial orientation (Acredolo, 1978; Acredolo & Evans, 1980; Bremner, 1978a; 1978b; Meuwissen & McKenzie, 1987) suggests a visual component to performance. However, the fact that infants (Lew, Foster, & Bremner, 2006) and toddlers (Hermer & Spelke, 1996), have difficulty using landmarks following inertial stimulation raises the possibility that the updating process, whether to landmarks or hidden goal, is at least partially based on vestibular input.

In addition, evidence that young infants are capable of taking account of body rotation in featureless environments (Lepecq & Lafaite, 1989; Tyler & McKenzie, 1990) has led to the suggestion that early spatial orientation is based on vestibular input (Tyler & McKenzie, 1990). However, in the absence of landmarks, body rotation gives rise to visual flow information event in finely textured environments. And it has been demonstrated that visual flow simulating linear body movement affects postural stability. Lee and Lishman (1975) showed that if adult participants were put in a moving room in which the floor was stable but the walls moved, they reported the feeling that it was they who were moving rather than the walls. Lee and Aronson (1974) found that when placed in the moving room infants who had just learned to stand upright fell over when the walls moved, and Butterworth and Hicks (1977) obtained evidence for adjustment of sitting posture resulting from wall movement from nine– and eighteen–month–old infants. Further work indicates developmental changes in the amount of visual flow needed to trigger postural adjustment, with 7-month-olds requiring global flow whereas peripheral or central flow is sufficient at 9 months (Bertenthal & Bai, 1989), and also in the degree of attunement to optical flow between 5 and 13 months (Bertenthal, Rose, & Bai, 1997). Thus it is clear that visual flow provides important information about postural stability, raising the possibility that it is also important in the maintenance of heading. And it is possible that visual flow information was used for spatial orientation in Tyler and McKenzie's task, despite the absence of distinct landmarks.

The literature on animal and human maintenance of heading does not lead to a clear conclusion regarding the likely basis of infant spatial orientation. Some work on path integration and maintenance of heading suggests that vestibular information is of primary importance in both animals (Stackman & Herbert, 2002; Wallace, Hines, Pellis, & Whishaw, 2002) and humans (Cohen, 2000; Klatsky, et al., 1998; Simons & Wang, 1998) and the disruption produced by inertial disorientation without vision on toddlers' performance (Hermer and Spelke) might point to a primarily vestibular basis for infant spatial orientation. However there also is growing evidence that adults can use visual information alone for spatial updating during rotational transformations (Riecke, von der Heyde, & Bülthoff, 2004; 2005) and that they use optical flow preferentially in navigating visually rich environments (Bruggeman, Zosh, & Warren, 2007). Furthermore, there is considerable evidence that, rather than using one sensory channel preferentially, adult humans (Ernst & Banks, 2002) and monkeys (Gu, Angelaki, & DeAngelis, 2008) integrate information from different sensory channels in an optimal manner with the weighting given to different channels depending on their reliability (Ernst & Bűlthoff, 2004; Morgan, DeAngelis, & Angelaki, 2008). Such integration appears to be a general principle of adult intersensory perception, but applies in the specific case of integration between visual and vestibular channels. Cases in which one sensory channel appears to dominate appear to be explained by the fact that when sensory cues are disparate in the extreme, one will be discounted in favour of the other (Ernst & Banks, 2002).

However, integration of intersensory information appears to be relatively late in development. Gori, Del Viva, Sandini, and Burr (2008) found that optimal integration of haptic and visual form information only occurred at around eight years of age, and Nardini, Jones, Bedford, and Braddick (2008) found that, in contrast to adults, children up to eight years of age did not integrate vestibular and visual landmark information in navigation, tending to alternate between using one source of information or the other. This evidence suggests that although infants are unlikely to integrate information from visual and vestibular modalities in the way adults do, they may well be capable of using both sources of information, and questions exist concerning with sensory channel will be relied on in different situations and at different ages. Thus there is a clear need to investigate directly the relative contribution of vestibular and visual information in infant spatial orientation. The aim of the present research is to begin to address this issue through a series of studies in which Lee and Lishman's methodology is adapted to make it applicable to spatial orientation testing. Using Tyler and McKenzie's basic technique, infants are trained to anticipate the appearance of a fixed event within a cylindrical enclosure. Following training, several forms of test trial are presented so as to isolate or put in opposition visual flow and vestibular information. Specifically, if the surround is rotated rather than the infant, only visual information for movement is provided. Or if the surround and infant are rotated simultaneously, only vestibular information is provided. Finally, if both infant and surround are rotated in the same direction, but the latter at twice the rate, vestibular information specifies one direction of rotation and visual flow information the opposite direction of rotation.

In the main studies we tested infants between the ages of 6 and 14 months, this being the age range that has been the focus of most prior research. However, it seemed important to provide an adult baseline. Previous research has investigated the effects of visual and vestibular information on adults' sense of body position, orientation (Ivanenko, Grasso, Israel, & Berthoz, 1997; Wertheim, Mesland, & Bles, 2001) heading (Blouin, Gauthier, & Vercher, 1995), and subjective impressions of rotation (Wong & Frost, 1981), and also on their control of arm movement in pointing to a target (Guillaud, Gauthier, Vercher, & Blouin, 2006). However, these studies either investigate perception and motor adaptation during the sensory stimulation itself rather than on spatial orientation following stimulation. And when they do investigate spatial orientation they tend to compare performance with and without vestibular (Riecke et al., 2004) or visual information (Rieser, Ashmead, Talor, & Youngquist, 1991) and so do not make all the comparisons we have in mind here. Thus we began our investigation with an adult version of the infant task.

Experiment 1

The aim of this experiment was to evaluate the relative contribution of visual flow versus vestibular information in a task requiring adults to relocate a target following movement. Because the purpose was to provide an adult baseline for subsequent infant experiments, the task was designed so as to be easily adaptable for use with infants. Four conditions were run, a baseline condition and three others that manipulated visual flow information and vestibular information for bodily rotation separately or in combination.

Method

Participants. Forty-eight adults, 38 female and 10 male in the age range 20-30 years took part in the study. Twelve were assigned to each of the four conditions in such a way as to ensure that the mean age and gender balance were comparable across conditions.

Apparatus. The experimental environment consisted of a circular enclosed room with a chair at its centre. The entire room was raised 26 cm from the ground, and was 244.2 cm in diameter and 191.5 cm in height, from floor to ceiling. The chair seat was 57 cm above the floor of the enclosure. The room was lined internally with off white opaque fabric, forming the cylindrical wall of the room. This was divided by 9 openable elasticized vertical slits extending from floor to ceiling at 30-degree intervals over a total angle of 240 degrees. Three movable video cameras were attached at a height approximately equivalent to participants' eye level to a support rail outside the material wall, to monitor and record participants' head and eye movements. To ensure that the sites at which the cameras were positioned were not distinctive, six false camera lenses were placed at the remaining sites. The fabric was stretched over a frame, eliminating sway during rotation but resulting in minor uniform undulations top to bottom that provided shading texture in the surround. Nine red LED lights were positioned at each of the nine sites directly above the camera positions, which were adjacent to the elasticized slits. The resulting texture and uniformly spaced features provided noticeable visual flow information when participant or surround was rotated. The lights could be activated singly from outside the circular room. Once activated the light flashed in order to attract participants' attention. A television monitor and three-channel mixer located outside the circular room and near the event site, allowed the experimenter to monitor the participants' responses via the three cameras.

The chair was mounted on a central bearing that could be rotated by the experimenter. The enclosure was also connected to this central bearing, allowed it to be rotated as a whole. A belt system could be engaged that locked chair and surround together, either so that they rotated in the same direction at the same rate or so that the surround rotated at twice the speed of the chair. In these cases, the combined movements were achieved by the experimenter rotating the surround manually. All rotations occurred soundlessly.

Design. The aim of evaluating the relative contribution of visual flow information versus vestibular information was achieved by measuring adults' estimation of the position of a fixed target location following four different types of spatial transformation. Because the purpose was to provide an adult baseline to which infant performance would be compared, we adopted the same basic procedure as used by Tyler and McKenzie with infants, in which initial training involved learning to anticipate appearance of a target at a fixed location from two directions of facing, followed by a single test trial. The test trial involved a transformation that provided either congruent or conflicting information in the visual and vestibular modalities. The form of the test trial differed for each of the four groups of participants. A *baseline condition* similar to the test trial used by Tyler and McKenzie (1990) contained both visual and vestibular information of movement to a new direction of facing (see figure 1), a *visual change condition* provided only visual information of movement, a *vestibular change condition* provided only vestibular information of movement, and an *opposed visual and vestibular condition* provided visual and vestibular information specifying equal but opposite directions of rotation. These test trials were designed so as to make it possible to establish the relative contribution of vestibular and visual information to participants' response, and whether this varied dependent on whether vestibular and visual information for movement where presented in isolation or in opposition.

Procedure. The target event was the appearance of the experimenter at one of the elasticized slits between the panels of the enclosing wall. Only her head was visible. The appearance occurred at the same fixed location in the laboratory frame for every trial. Participants were provided with a pointer to point to the position at which they anticipated the event would appear. They were instructed not to point to the event site on the first trial, but to point as accurately as possible on subsequent trials, and to touch the material of the wall, so that the experimenter could mark the position. They were told that they would be rotated to different positions and that, after the practice trials, the event would occur in the same place in the laboratory frame each time. No other instructions were given.

Participants received two practice trials and six training trials. To ensure that participants had no prior knowledge of event site or chair positions before the experimental trials, both the practice trials and the practice event site were different from those used in training and test. The chair was manually rotated to the first practice position, 30, 60, or 90 degrees to the right or left of the starting point. To cue the start of the trial the light in front of the participant flashed for three seconds, and two seconds later the experimenter appeared at the target site. A transformation phase followed in which the chair was rotated to the next practice position, past the event site and 120 degrees from the first training position. Again, to signal the start of the trial the light in front of the participant was activated for three seconds, and this time the participant was asked to point to the anticipated event location (target). Two seconds following the participant's point, the experimenter appeared at the event location.

The training sequence is illustrated in Figure 1. Before the first training trial, the participant was oriented to face the target site used during training and test. The chair was then manually rotated to the first training position, 60 degrees to the right or left of the target direction. The light in front of the participant flashed for three seconds to cue the start of the trial. The participant was asked to point to the anticipated event location (target), and two seconds later target feedback was provided by the experimenter appearing at the target site. A transformation followed in which the chair was then rotated clockwise or anticlockwise to the next training position, past the event site and 90 degrees from the first training position (thus 30 degrees to right or left of the event site). Following this, the light in front of the participant was activated for three seconds to cue the start of the next trial, whereupon the participant pointed to the anticipated position of the target. Again, the experimenter appeared at the event site two seconds after the participant had pointed. This procedure was repeated until the participant had received a total of six training trials, three from each side of the target event site (Training from two directions of facing is typically used in infant work to prevent establishment of perseveration of a single response.).

The single test trial followed immediately. The form of the transformation in this trial differed between conditions, as indicated in Figure 2. To allow measurement of anticipatory looking the experimenter did not appear at the target position. In the *baseline condition*, the chair was rotated past the target event site and 60 degrees from the last training position to a new test position (30 degrees to right or left of the event site), providing both visual and vestibular information for a change in orientation. In the *visual change condition*, the room was rotated 60 degrees clockwise or anti clockwise, whilst the chair remained stationary in the position of the last training trial. This provided visual flow information but no vestibular information for a change in orientation. If the last training trial had occurred with the participant oriented to the left of the target event site, the room was rotated anticlockwise (generating the visual flow direction that would result from a clockwise body rotation), and if to the right, the room was rotated clockwise. In the *vestibular change condition*, the chair was rotated 60 degrees past the target event site, and the room was simultaneously moved 60 degrees in the same direction (chair and surround were locked together in this condition, allowing no movement of the chair relative to the surround). This provided vestibular information but no visual information for a change in orientation. If the last training trial had occurred to the left of the target event site, the room and chair were rotated clockwise, and if to the left, they were rotated anticlockwise. In the *opposed visual and vestibular condition*, the chair and the room were also rotated simultaneously but through different extents. The chair was rotated 60 degrees past the target event site, and the room was rotated 120 degrees in the same direction. This provided visual flow information for a change of orientation in one direction and vestibular information for a change in the opposite direction. If the last training trial had occurred with the participant oriented to the left of the target event site, chair and surround were rotated clockwise, and if to the right, they were rotated anticlockwise. All chair and surround rotations took place at a peak velocity of approximately 45 degrees/sec, with smooth acceleration and deceleration phases during the approximately the first and last 15 % of the movement, apart from the test trial in the surround-twice-self condition in which the surround was rotated at a peak velocity of approximately 90 degrees/sec and the chair at half that rate.

Following each of these transformations, the cue light in front of the participant was activated for 2 seconds, whereupon the participant pointed to the anticipated location of the target. In each condition, the locations were identified that participants could be expected to point to depending on whether they were relying accurately on visual or vestibular information. In all but the *baseline condition,* reliance on vestibular or visual information predicted opposite directions of updating and different locations at which event prediction should occur. Note that reliance on vestibular information in the *visual change condition* and on visual information in the *vestibular change condition* would result in perception of no change in orientation and thus would result in an anticipatory look in the same direction as on the last training trial. To allow comparison with infant responses, participants' point locations were coded as accurate according to vestibular or visual information if they fell within an area 15 cm either side of the slit in the curtains at a particular site and between 50 cm from the roof of the circular room and 80 cm above the floor, and area corresponding to that taken up by the appearance of the investigator during training. Any other responses were coded as angular departures from whichever target location (visual or vestibular) they were closest to.

Results and discussion

In the baseline condition visual flow and vestibular information specified the same rotation and hence would be expected to prompt identification of the same target location. All other conditions were designed so that reliance on visual information would lead to identification of the target at a specific position to one side of midline whereas reliance on vestibular information would lead to identification of the target at a specific position to the opposite side of midline. Table 1 displays the data coded for both directional and positional accuracy. The directional measure is strikingly clear: the overwhelming majority of participants looked in the direction specified by visual flow. The only exception was one individual in the *vestibular change condition* who pointed straight ahead. The more exact criterion for location (15 cm either side of the surround slit) also yielded very clear data. All but three of those who had pointed in the direction specified by visual information pointed at the target location specified by visual information. It is noteworthy that all those who did not were in the *opposed visual and vestibular condition*. These three individuals pointed to the location 30 degrees closer to midline than that specified by reliance on visual flow information, an outcome in keeping with a small effect of vestibular information. Otherwise, the majority of participants responded in terms of visual flow information and appeared to show no awareness of the conflict between visual and vestibular information.

The striking finding is that in all conditions other than the baseline condition*,* the majority of participants were pointing at a location that was 60 degrees away from the actual target location. In other words, participants' reliance on visual flow information made them very poor at identifying a fixed position within the laboratory framework. Given that participants were informed that the target was stable within the laboratory frame, it seems unlikely that they were solving the task by assuming that the target moved with the surround, and these results are consistent with adults discounting information from one sensory channel (in this case vestibular information) when it is markedly incongruent with information from another channel (Ernst & Banks, 2002)

These data are so clear that statistical analysis was unnecessary. It would have been possible to analyse pointing angles more precisely to detect whether there were subtle effects across the different conditions that suggested subsidiary effects of vestibular information for movement or stability.

However, the aim here was to provide an adult baseline for the infant work, and the 15 cm error margin allowed here is reasonable given that it corresponds to target size, and is of a similar level of accuracy as is likely to be possible from scoring infant looking direction.

Experiment 2

Having established how adults respond in this task, we moved to investigating infants' performance in the same conditions used in Experiment 1. In this case, the dependent measure, in parallel with work by McKenzie and colleagues, was anticipatory looking on the test trial. But apart from the lack of verbal explanation given to adults, essentially the same procedure was followed as in Experiment 1. In order to investigate possible developmental change, we tested groups of infants of mean age 7, 9, and 12, covering the age range 6 to 14 months.

Method

Participants. A total of 216 infants took part in the experiment: 72 6- to 8-month-olds (*M* = 213.3 days; range 184 – 240 days; 36 girls and 36 boys), 72 8- to 11-month-olds (*M* = 279.4 days; range 244 – 332 days; 36 girls and 36 boys), and 72 12- to 14-month-olds (*M* = 371.5 days; range 349 – 428 days; 35 female and 37 male). A further 36 infants failed to complete the session due to fussiness. Within each age group, 18 infants were assigned to each of the four experimental conditions in such a way as to ensure that the mean age and gender balance were comparable across conditions.

Apparatus. The same equipment was used as in Experiment 1, with the addition of a VCR to record images of the infant captured by the three cameras. In order to maximize the accuracy of judgment of gaze direction, camera positions were varied depending on condition so that, following the test trial manipulation, one camera was always at the infant's straight ahead viewing point, and the other two were at the fixation points predicted by reliance on visual flow and vestibular information respectively. The first camera was used to detect direction of look, whereas the other two were used to estimate accuracy of fixation of the points specified by visual and vestibular information respectively.

Procedure. The procedure was largely the same as in Experiment 1, but was adapted in places to make it appropriate for infant testing. A short play session of about five minutes took place in the enclosure before testing commenced, so that the infant became accustomed to the surroundings and the investigator.

All infants received a total of eight training trials, four from each direction of facing. The parent was directed to sit on the chair in the centre of the room with her/his feet on the footrest. The infant sat on the parent's knee, facing forwards. The seat of the chair was 57 cm from the floor, so that when seated on the parent's lap the infant's eye level was approximately the same as the camera heights. Parents were asked to remain looking forward at all times, and were asked not to communicate with their infant in any way. Before commencement of the first trial, the parent and infant were seated facing the target site. The chair was then rotated to the first training position, 60 degrees to the left or right of the starting point (see figure 1). At the start of the trial, the light facing the infant flashed until the infant was fixating it. Immediately following this the experimenter appeared at the target site, saying "Boo. Here I am. Hello...(child's name)" A transformation phase followed in which the chair was then rotated to the next training position, past the event site and 90 degrees from the first training position (hence 30 degrees to right or left of the event site). Once this movement was complete the next trial commenced with the light cue in front of the infant, followed by the target event. The target event occurred at the same location in the laboratory frame of reference for every trial. This procedure was repeated until the infant had received a total of eight training trials, four from each side of the target event site.

The single test trial followed immediately. The transformation phase of the test trial differed between conditions, and to allow measurement of anticipatory looking the experimenter did not appear at the target position following the light cue. In the *baseline condition* (see figure 2), the chair was rotated past the target event site and 60 degrees from the last training position to a new test position (30 degrees to left or right of the event site). In the *visual change condition*, the room was rotated 60 degrees clockwise or anti clockwise, whilst the chair remained stationary in the position of the last training trial. In the *vestibular change condition*, the chair and the room were rotated simultaneously, 60 degrees clockwise or anti-clockwise past the target event site. In the *opposed visual and vestibular condition*, the chair was rotated 60 degrees clockwise or anticlockwise past the target event site, and simultaneously within the same time span the room was moved 120 degrees in the same direction. In all cases, following the test trial spatial transformation, the straight-ahead light cue flashed until the experimenter verified from the video data that the infant was fixating it. Measurements of anticipatory gaze direction followed once the light stopped flashing.

Predictions. The results of Experiment 1 indicated that adults relied overwhelmingly on visual information, whether this specified movement or stability, and that this reliance was maintained even when vestibular information specified an opposite direction of movement. This is consistent with strong effects of visual information on postural stability in adults and infants, and it might be assumed that infants should show similar reliance on visual information in the present task. However, predictive orientation to a target is fundamentally a different behaviour from maintenance of postural stability, and it is not certain that we should predict the same effect in spatial orientation. Our finding with adults is consistent with the conclusion that when there is a large disparity between information from two sensory channels, adults discount information from one sense. However, work with children suggests that discounting does not occur, and in a navigation task children tend to alternate between using one sensory channel and the other (Nardini et al, 2008). If this is also true of infants, we would expect to find less consistency in responding in the three conditions in which vestibular and visual information is incongruent than in the *baseline condition* in which information about movement is congruent across the senses. Secondly, if infants are sensitive to both visual and vestibular information, we might expect response consistency to be lower in the *opposed visual and vestibular condition*, in which vestibular and visual information specify opposite movements, and in the *visual change* and *vestibular change* conditions in which one sensory channel specifies a movement and the other specifies stability. Finally, although infants may be sensitive to both vestibular and visual information, one source of information may have more influence than the other, and this may vary depending on how visual and vestibular information is combined in the different test conditions. On this, we can make no clear prediction; although Tyler & McKenzie (1990) suggest that vestibular information is primary, indirect evidence suggests sensitivity to both visual and vestibular information, but gives no pointers to whether one source should have more influence than the other.

Measures and coding. Recognising that infants might look to more than one location on the test trial, Tyler and McKenzie (1990) measured both direction of first look and total duration of looking to target within a 5 second period following onset of the first look. In their work these measures yielded essentially the same outcomes. However, in the present work, particularly in conditions in which visual and vestibular information were uncorrelated, it was evident that many infants looked to more than one location during the test trial. Thus, we judged that a long look should be a more reliable indicator of sustained trained anticipation than a fleeting first look. Also, we found that longest looks tended to be quite sustained, averaging 2.27 s across ages and conditions, and their analysis yielded similar outcomes to analyses based on the total duration of looking measure used by Tyler and McKenzie. Two measures were derived from longest look data. Firstly, looks were coded simply for *direction*. In the baseline condition this involved recording the number of infants who looked towards the target. In the other conditions, this involved recording the number of infants who looked in the direction specified by visual flow versus the number that looked in the direction specified by vestibular information. Because the two sources of information always specified opposite directions of looking, and because no infants looked straight ahead, all infants fell into one of these categories. Secondly, looks were coded according to a stricter *location* criterion. Because there were camera and light positions every 30 degrees, most infants looked quite directly at one of these positions. However, all looks were coded in terms of which of these positions was most closely fixated, and the number of infants looking to target was recorded. In the baseline condition, this involved recording the number of infants whose fixation was closer to the actual target than other locations. In the other conditions, this involved recording the number of infants who looked to the target as specified by visual flow and vestibular information respectively. Our reason for adopting these two criteria was that it is possible for infants to use visual and/or vestibular information at two levels; a) to simply identify *direction* of movement and b) to identify *direction and extent* of movement.

In this experiment and the two that follow, 20% of video records were scored by a second scorer naïve to the aims and hypotheses. Inter-scorer reliability was high, with 91% agreement on exact measures and 95% agreement on directional measures.

Results

Table 2 displays the data, subdivided by age and condition. For both directional and location codings, a binary logistic model was fitted to the data using the Generalised Linear Interactive Modelling (GLIM) Package (Francis, Green, & Payne, 1993). In each case, the model was first constructed by adding each factor (Age and Condition) individually. Then, changes in deviance were assessed by addition of the interaction between factors to the model.

The first set of analyses included the data for the *baseline condition*, to provide a reference for performance in the other (experimental) conditions. In these analyses, we were interested in two things, firstly how performance in the experimental conditions compared to that in *the baseline condition*, and secondly whether performance in the *baseline condition* varied as a function of age. Thus we report condition and age effects for the whole data sets and just age effects for the *baseline condition*. However, given that the *baseline condition* confounds vestibular and visual information, further analyses to tease apart vestibular and visual effects were also carried out omitting the *baseline condition*.

Analyses including baseline condition.

The directional measure yielded a significant condition effect, χ^2 (3, $N = 216$) = 27.15, $p < .0001$. Responding was more consistent across infants in the *baseline condition* than in the *visual change condition,* χ^2 (1, $N = 108$) = 20.0, $p < .0001$, the *vestibular change*, and *opposed visual and vestibular conditions*, χ^2 (1, $N = 108$) = 14.66, $p = .0001$, and there were no other differences in performance between conditions, χ^2 (1, $N = 108$) .15, $p = .69$. The age x condition interaction was not significant, χ^2 (6, $N = 216$) = 7.42, $p = .28$. There was no significant difference in performance on the *baseline condition* between the three age groups, χ^2 (2, $N = 45$) = .53, $p = .77$.

The location measure yielded a significant condition effect, χ^2 (3, $N = 145$) = 51.67, $p < .0001$, and the data suggest this arose from more consistent responding in the *baseline condition*. However, parameter estimates and standard errors were inflated, so this effect cannot be interpreted with confidence. The age x condition interaction was not significant, χ^2 (6, $N = 145$) = 1.96, $p = .92$. There was no significant difference in performance on the baseline condition between the three age groups, χ^2 (2, $N = 36$) = 2.67, $p = .26$.

In summary, performance on the direction measure was more consistent in the baseline condition than in the experimental conditions, and there were no age effects in performance on the baseline condition on either measure. The same appeared to be true of the location measure, though the condition effect was hard to evaluate statistically.

Analyses omitting baseline condition.

The directional measure yielded a significant age effect, χ^2 (2, $N = 216$) = 14.07, $p = .0008$. There was no difference in performance between 7- and 12-month-olds, χ^2 (1, $N = 108$) = .16, $p = .69$, but there was significantly more vestibular responding by 9-month-olds than by both 7-month-olds, χ^2 (1, $N = 108$) = 10.72, $p = .001$, and 12-month-olds, χ^2 (1, $N = 108$) = 7.26, $p = .007$. The condition effect was not significant, χ^2 (2, N = 216) = .45, p = .79, and the interaction between age and condition was not significant, χ^2 (4, N = 216) = 7.15, p = .13.

The location measure yielded a significant age effect, χ^2 (2, N = 110) = 8.05, p = .018. There was no difference in performance between 7- and 12-month-olds, χ^2 (1, N = 70) = .006, p = .94, but there was more vestibular responding by 9-month-olds than by both 7-month-olds, χ^2 (1, N = 71) = 4.89, p = .027, and 12-month-olds, χ^2 (1, N = 77) = 4.68, p = .03. There was also a significant condition effect, χ^2 (2, N = 109) = 9.25, p = .01. There was no difference in performance between the *visual change* and *vestibular change conditions*, χ^2 (1, N = 80) = .02, p = .89, but there were significantly fewer accurate looks in the *opposed visual and vestibular condition* than both the *visual change*, χ^2 (1, N = 70) = 5.37, p = .02, and *vestibular change* conditions, χ^2 (1, N = 68) = 5.7, p = .017.

In summary, for both the direction and location measures, there was more vestibular responding at 9 months and more visual responding at other ages. Additionally, across all ages and relative to other conditions fewer infants in the *opposed visual and vestibular condition* satisfied the more precise location criterion, whether specified by visual or vestibular information.

Discussion

On the directional measure in particular, infants are more accurate in the baseline condition than the other conditions in which vestibular and visual information are manipulated independently. Although the condition effect for the location measure was hard to interpret due to the nature of the data, it appears that the same trend was present on that measure. At first sight, such a finding might seem predictable: when visual and vestibular information combine to specify the same location, performance could be expected to be better. However, the result is important in comparison with adult performance in Experiment 1, which was overwhelmingly guided by visual information. Thus, even though infants showed a clear tendency to rely more on one type of information, at no age is it such a strong tendency as to be uninfluenced by absent or conflicting information from another sensory channel. In addition, the fact that accurate looks were less frequent when visual and vestibular information were in opposition (*opposed visual and vestibular condition*) provides evidence for partial reliance on both sources of information by all infant age groups.

The difference in results for adults and infants is in keeping with the conclusion that adults discount information from one sensory channel when it is particularly disparate from that in another (Ernst & Banks, 2002) whereas children are sensitive to both vestibular and visual information but do not integrate optimally (Nardini et al., 2008) and do not discount disparate information. However, the particularly low frequency of accurate looks in the *opposed visual and vestibular condition* suggests that responding in this task is not guided by one source of information or the other, but by a non-optimal integration of both.

The most striking finding is that, whereas the youngest and oldest age groups responded predominantly according to visual flow information, the 9-month-old group responded predominantly according to vestibular information. What might be the reason for this different and unexpected finding at 9 months? A possible explanation can be found in the literature on the effects of locomotion on spatial cognition. It is argued that the onset of locomotion leads infants to expect systematic correlations between kinaesthetic information about locomotion, visual, and vestibular input (Bertenthal & Campos, 1990; Campos et al. 2000). From this perspective, the relative salience of visual and vestibular information might be different in the period (around 8 to 9 months) during which infants are becoming mobile. We shall return to this issue in the general discussion.

Experiment 3

If calibration between body movement information, and vestibular and visual information is reaching new levels during the period when the infant is gaining independent mobility, we must assume that infants can use vestibular information at least by that age. Also, the evidence from 7-month-olds in

Experiment 2 suggests some influence of vestibular information that leads to rather inconsistent responding across conditions. The question that follows from this is whether younger infants are capable of using vestibular information in a consistent way in spatial orientation. To investigate this we probably need a more sensitive test than included in the current set of conditions. In the *vestibular change condition*, vestibular information for body rotation is present, but visual information specifies non-movement. Although visual information predominates in this condition, that does not mean that infants could not use vestibular information if visual information did not conflict with it. Thus in Experiment 3 we repeated the *vestibular change condition* but turned off the lighting during the test transformation. This achieved our aim of presenting vestibular information for movement with no conflicting visual information.

Method

Participants. Eighteen 6- to 8-month-olds (M = 204.6 days; range 183 – 241 days; 10 girls and 8 boys) took part in the experiment. A further four infants did not complete testing due to fussiness.

Apparatus & procedure. The same experimental environment was used as in Experiment 2, with the cameras mounted in the positions used in the *vestibular change condition* of Experiment 2. The procedure was also the same, except that the enclosure lighting was extinguished for the duration of the test trial transformation.

Results and discussion

Table 3 displays the direction and location results. These data were analysed relative to chance and relative to comparable conditions in Experiment 2. On the directional measure, a significant majority of infants look in the direction specified by vestibular information (*binomial* p = .048). The most marked increase in use of vestibular information relative to the *vestibular change condition* of Experiment 2 is on the directional measure, though this difference is not significant, χ^2 (1, N = 36) = 1.83, p = .18. However, there is a significant difference on this measure between the present experiment in which only vestibular information for movement is provided and the *visual change condition* of Experiment 2 in which only visual information for movement is provided, χ^2 (1, $N = 36$) = 9.11, $p = .0025$.

This study provides evidence that the youngest infants are capable of using vestibular information for movement provided visual information does not specify absence of movement. The effects of vestibular and visual information are not symmetrical, however, because infants in the *visual change condition* of Experiment 2 showed strong reliance on visual information even though vestibular information specified no movement. There are two possible reasons for this asymmetry. Firstly, vestibular information may be less salient than visual information for this age group. Secondly, beyond considerations of salience, a stable visual field possibly provides more direct positive information for stability than a lack of vestibular input.

Experiment 4

In the final study we turned to clarification of the predominantly vestibular responding by the 9-month-old group in Experiment 2. There seems to be no basis for concluding that this occurred because the visual flow information arising from structure and texture in the surround was insufficient to be detected by this group. However, we can test the strength of the vestibular tendency by enhancing visual information for movement. If the vestibular tendency were particularly strong we would expect little or no effect of enhancing visual information, whereas if we are dealing with the outcome of relative salience of different forms of information, enhancement of visual information might produce a significant shift to visual responding.

The *opposed visual and vestibular condition* in Experiment 2 provided strongest evidence of vestibular responding by the 9-month-old group. Thus in Experiment 4 we presented this condition to a group of 8- to 10-month-olds, enhancing visual differentiation by attaching black discs to the surround.

Method

Participants. Eighteen 8- to 10-month-old infants ($M = 272.9$ days; range 247-314 days; 7 girls and 11 boys) took part in the experiment. A further three did not complete testing due to fussiness.

Apparatus & procedure. The same experimental environment was used as in previous experiments, with the addition of 24 black fabric discs, measuring 25cm in diameter. The discs were attached to the walls of the circular room at 30-degree intervals, the centres half way between each camera lens. The discs were attached in two rows, with the centres of the top row 45cm from the roof of the room and those of the bottom row 70cm from the floor of the room. This arrangement ensured that none of the discs provided the infants with a beacon landmark to the target location. The camera mountings and the experimental procedure were the same as in the *opposed visual and vestibular condition* of Experiment 2.

Results and discussion

Table 4 displays the direction and location results. Although the vestibular tendency is somewhat reduced relative to the equivalent condition in Experiment 2, vestibular responding still predominates. On neither measure is there evidence of a significant reduction in vestibular responding relative to Experiment 2 as a result of the enhanced visual flow information, *direction*, χ^2 $(1, N = 36) = 0.12$, $p = .73$; *location*, χ^2 $(1, N = 36) = 0.36$, $p = .55$. Despite provision of very clear information for visual flow, 9-month-olds continued to respond predominantly on the basis of vestibular information. The absence of any clear evidence of response to what might be assumed to be highly salient information for visual flow is striking and adds support to the conclusion that this age group is responding in a very different way from 12-month-olds and adults.

General Discussion

In common with adults, 7- and 12-month-olds in Experiment 2 responded predominantly to visual flow information. However, unlike adults, they showed different performance relative to baseline in conditions in which visual and vestibular information were not coordinated, particularly on the location measure in the condition in which visual and vestibular information were in direct opposition. This suggests partial sensitivity to information in both modalities rather than the total reliance on visual information seen in adults, and Experiment 3 shows that 6-month-olds use vestibular information when there was no conflicting visual information. The most striking finding is the predominance of vestibular responding by 9-month-olds, which persists even when visual information is enhanced (Experiment 4). The findings of Experiment 2 are of primary importance and also provide the greatest theoretical challenge. In particular, why do 9-month-olds rely primarily on vestibular information whereas 12-month-olds and 7-month-olds rely primarily on visual flow information?

Firstly, we conclude that this effect is specific to spatial orientation, because no such developmental pattern is evident in the case of maintenance of posture, in which visual flow information appears to primary at all ages tested (Bertenthal & Bai, 1989; Bertenthal et al., 1997; Butterworth & Hicks, 1977; Lee and Lishman, 1975). To understand our effect, it may help to consider the forms of spatial orientation that infants are likely to be engaged in, both before and after the onset of locomotion. Interpretations of spatial orientation and maintenance of heading tend to be couched in terms of infants constructing new ways of organising space that are appropriate for their newfound postural or motor capabilities (Bremner, 1993; Bremner & Bryant, 1985; Newcombe & Huttenlocher, 2000). And other approaches portray children and adults as engaged in processes of calibrating perceptual information in relation to action (Pick, Rieser, Wagner, & Garing, 1999; Rieser, Pick, Ashmead, & Garing, 1995). In both cases, action is central to development, and investigating spatial cognition in relation to developing action may provide the best means of explaining the present data.

Two milestones in development may be particularly important. Once infants can sit unaided (at around 6-7 months) they are able to inspect the world through controlled movements of eyes, head, and trunk. It has been argued elsewhere (Bremner, 1993; Bremner & Bryant, 1985; Newcombe & Huttenlocher, 2000) that this may be an important milestone in spatial development, and those movements now under the infant's control bring about the same sorts of visual flow as occur in the current task. It is noteworthy that the vestibular sense provides good information regarding rotational accelerations of this sort (Bresciani et al., 2005; Ivanenko et al., 1997).

The analysis above explains how infants might gain the ability to take account of body rotation, but it does not explain the temporary dominance of vestibular information around 9 months. A possible reason for this arises from another milestone in motor development. The onset of locomotion has been widely identified as a likely contributor to various aspects of spatial ability (Bertenthal & Campos, 1990; Bremner, 1993; Bremner & Bryant, 1985; Clearfield, 2004; Horobin and Acredolo, 1986). Around nine months, most UK infants begin to crawl, and their attentional resources are likely to be focused on this new activity. We believe that it is possible to develop a plausible explanation of our developmental effect that relates to the onset of locomotion, though we recognise that, because we did not have data on the locomotor status of our infants at the time of testing, this explanation must remain tentative.

While crawling, visual and vestibular inputs are congruent, so one might assume that there is no advantage in departing from the previous reliance on visual information. However, Bertenthal and Campos (1990) argue that experiences accompanying the onset of independent locomotion lead infants to expect specific correlations between visual and vestibular information during locomotion. And, in time, they experience negative emotional reactions when the correlation is perturbed, such as when the infant approaches a visual drop-off (Campos et al., 2000). To become aware of correlations between visual and vestibular information it is likely necessary to attend to how both relate to kinaesthetic information about limb position and movement during locomotion. In consequence, vestibular information may acquire greater salience than earlier in development.

This, however, does not explain why this age group use vestibular information preferentially to visual information. A possible reason for reliance on vestibular information for heading during early locomotion arises from consideration of factors that contribute to variability of visual information.

Whereas vestibular information should be more less constant for a given rate of locomotion, visual information depends also on the structure of the environment. As pointed out by Campos and colleagues, visual flow information is perturbed when infants approach a drop off. Also, visual information is likely to be less salient in visually sparse environments, it having been shown that adults are less likely to use visual flow information under these circumstances (Bruggeman et al., 2007). Finally, the precise form of visual flow information will depend on the size and shape of the environment. These considerations suggest that, even if vestibular information for movement is subtle relative to visual information, constructing an active mapping between vestibular information and kinaesthetic information for movement may call on fewer resources because of the more or less constant relationship between the two. In contrast, the construction of a mapping to visual information is liable to be more complex through having to deal with variations in visual information resulting from differences in structure of the environments in which locomotion takes place, and its calibration to kinaesthetic information generated by movement may even depend on the presence of vestibular information that is unaffected by changes in environmental structure.

But why is there a shift to visual responding by 12 months? Once locomotion is achieved, there are at least two reasons why visual information can be expected to become dominant. Firstly, because the vestibular system is an inertial sensor stimulated by acceleration forces, it provides no direct information about linear velocity, and even vestibular information about linear accelerations is ambiguous, being confusable with body tilts (Wertheim, Mesland, & Bles, 2001). This provides good reasons why visual information would ultimately be relied upon more as a means of keeping track of translatory movements during crawling. Secondly, vision provides information regarding the spatial layout in which the infant is moving, whereas vestibular information does not. Thus, for the mobile infant, vision provides accurate information about displacements and the layout of the environment, effectively providing veridical information about the infant's orientation and movement in space.

We should not conclude that vestibular information about linear displacements is inferior to visual information in all respects. Although visual information provides better information about linear (constant) velocity, vestibular information provides better information for linear accelerations, and both forms of information may be important in the perception of linear movement (Schaffer & Durgin, 2005). The conclusion that both sources provide important information for movement is in keeping with the fact that, even at 12 months, there was evidence for at least some influence of vestibular information and with work indicating that adults tend to integrate intersensory information in an optimal manner (Ernst & Banks). One puzzle is why adults are so exclusively influenced by visual information in our task, particularly when the experimental manipulation involves just the form of rotational movements that the vestibular system seems well equipped to detect. The answer may be that in normal environments visual input provides veridical information about the relationship between the individual and environmental features, providing direct information about the spatial relationship between self and the targets of action. Thus it is likely to receive a higher weighting on the basis of its greater reliability (Ernst & Bűlthoff; Morgan et al., 2008) and when large disparities between visual and vestibular information are introduced, vestibular information is thus liable to be discounted.

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Footnote

1. Body movements are signalled by body pressure sensation as well as the vestibular system. It is not the aim to distinguish these sources and throughout the paper the term vestibular information is used to include both sources.

Figure Captions

Figure 1. A diagram to illustrate the two versions of the training sequence that applied in all conditions and the associated test trial in the baseline condition. The face symbol indicates the fixed location at which the experimenter appeared during training trials.

Figure 2. Test trial transformations for the four conditions in Experiments 1 and 2. The face symbol indicates the fixed location at which the experimenter had appeared during training. For simplicity, the transformations are illustrated for the case in which the final training trial took place with the participant oriented 30 degrees to the left of the appearance site.

Table 1

Number of participants (/12) in Experiment 1 pointing to target (Baseline condition) and to visual versus vestibular positions (other conditions), coded according to direction and location (±15 degrees of target) criteria.

	Rotation Condition						
Look coding	Baseline	Visual		Vestibular		Opposed Vis. & Vest.	
	target	vis.	vest.	vis.	vest.	vis.	vest.
direction	12	12	0	11	0	12	0
location	12	12	0	11	0	9	0

Table 2

Experiment 2: Number of infants (/18) making longest looks coded according to the direction and location (± 15 degrees) criteria relative to target (Baseline condition) and relative to visual versus vestibular positions (other conditions).

		Rotation Condition						
age	coding	Baseline	Visual		Vestibular		Opposed Vis. & Vest.	
		look direction/location						
		target	visual	vestibular	visual	vestibular	visual	vestibular
7m	direction	13	15	3	10	8	12	6
	location	12	9	3	7	3	4	6
9m	direction	17	8	10	5	13	6	12
	location	16	7	8	4	8	2	10
12m	direction	15	9	9	14	4	11	7
	location	8	8	6	13	4	2	5

Table 3

Number of infants (/18) making longest looks coded according to direction and location criteria relative to target in Experiment 3.

Measure	direction	location
longest look	13	5

Table 4

Number of infants (/18) making longest looks coded according to direction and location criteria relative to target in Experiment 4

Measure	direction		location	
	visual	vestibular	visual	vestibular
longest look	8	10	4	7

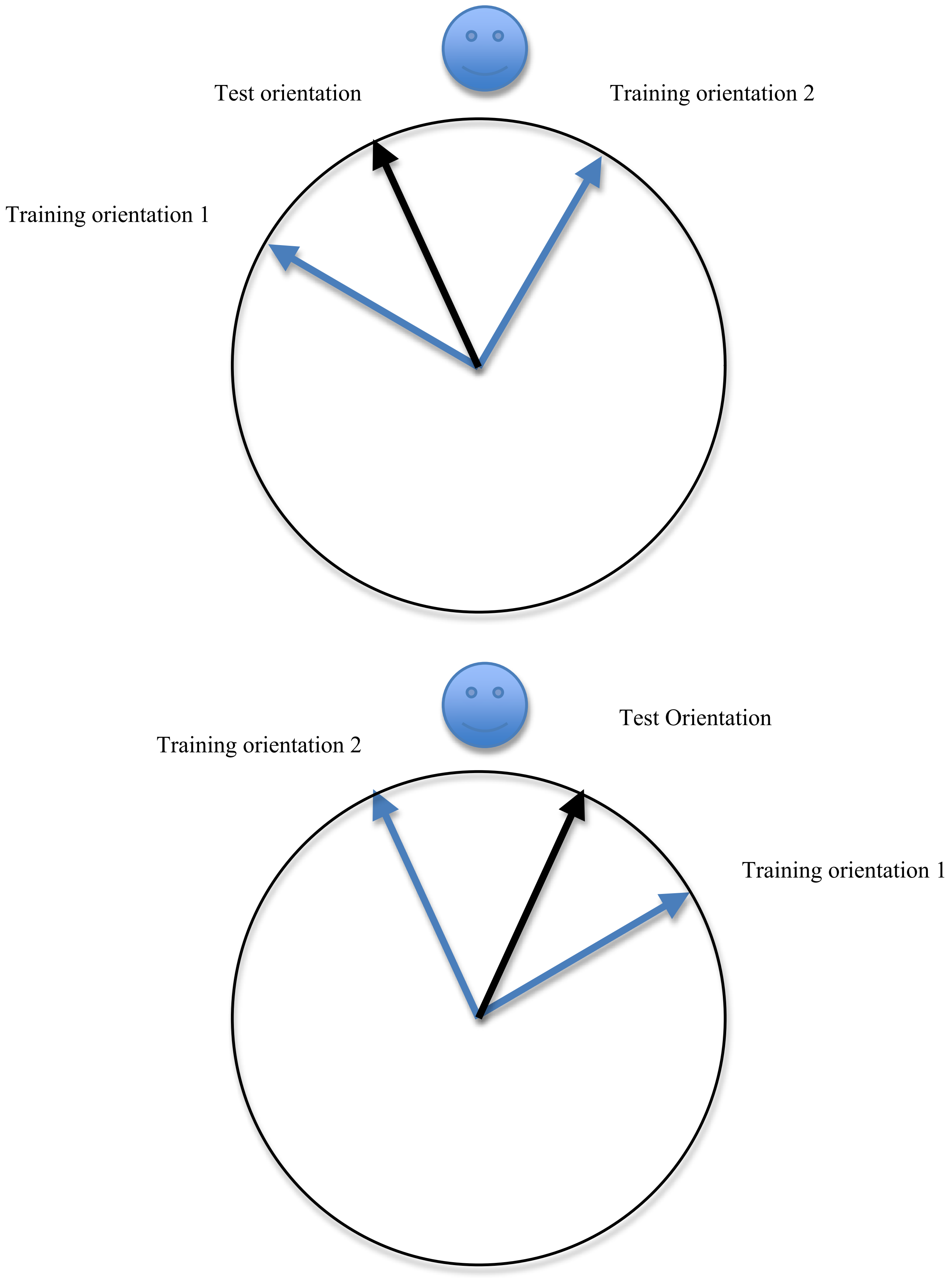
Test orientation
Training orientation 2
Training orientation 1
Training orientation 2
Test Orientation
Training orientation 1

Figure 1

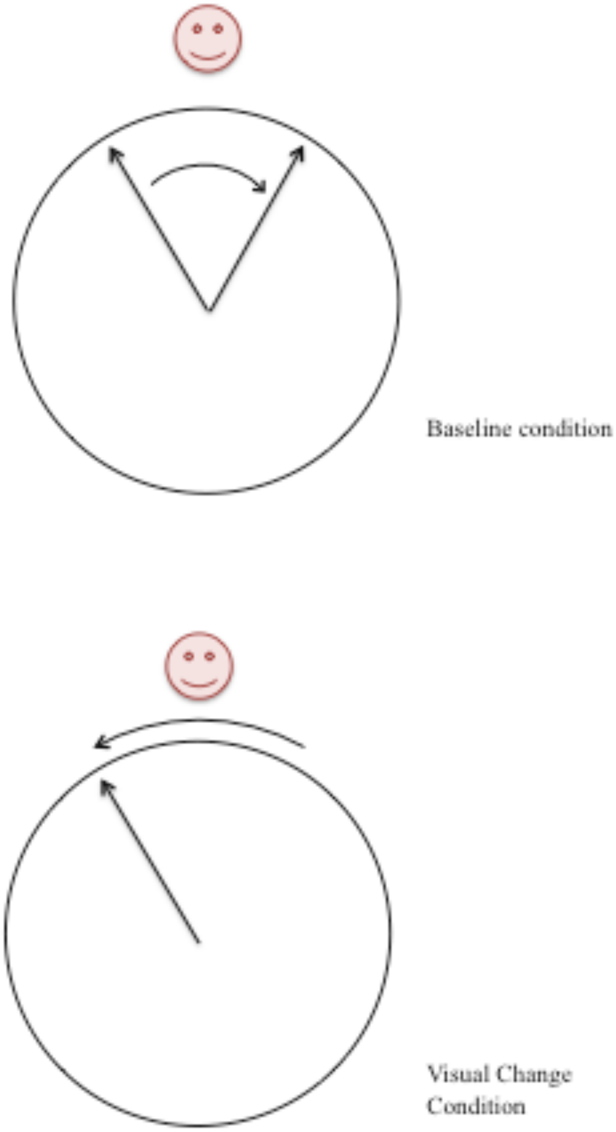

Figure 2 (a)

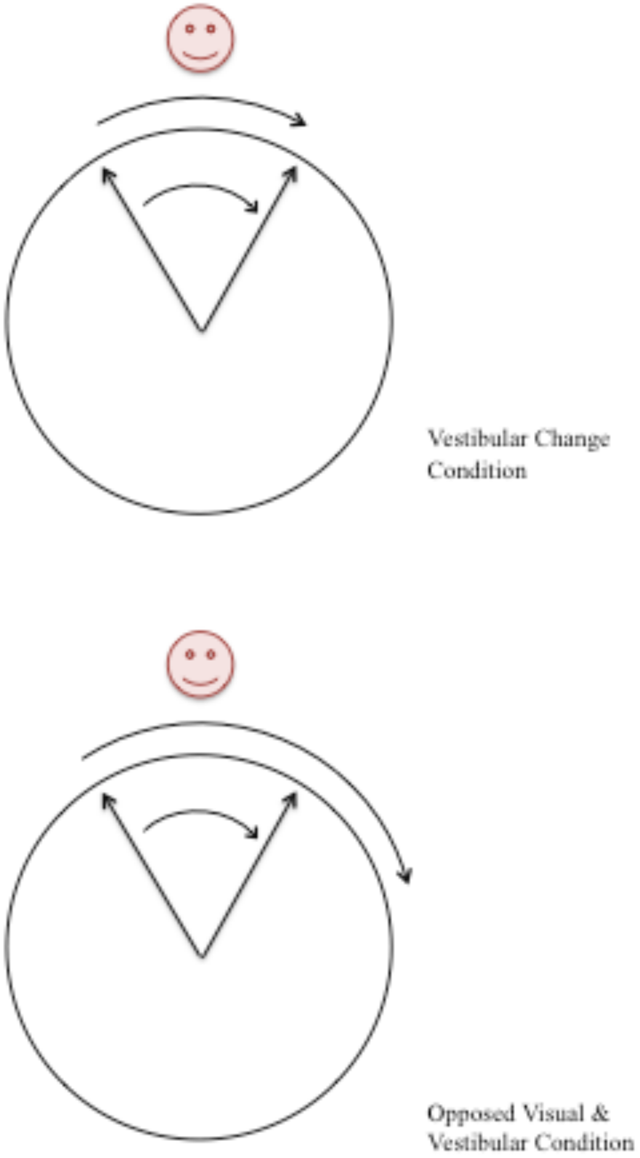
Vestibular Change Condition
Opposed Visual & Vestibular Condition

Figure 2 (b)