How children learn to deal with space: Developmental studies on spatial memory

Hoe kinderen leren omgaan met ruimte:
Ontwikkelingsonderzoek op het gebied van het ruimtelijk geheugen

(met een samenvatting in het Nederlands)

Proefschrift

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Voor mijn ouders

CHAPTER 1

GENERAL INTRODUCTION

General Introduction

1.1 Spatial cognition and spatial memory

Spatial cognition, the internalized reflection and reconstruction of space in thought (Hart & Moore, 1973), enables us to process all sorts of spatial information, e.g. orientation, location, distance, necessary for perceiving and remembering where things are and how to navigate from one place to the other. Spatial cognition is an important building block of general cognition and arguably could have been essential for how we evolved into the human beings we are today (Allen & Ondracek, 1995). That is, while several species of birds, mammals and nonhuman primates appear to possess clear spatial abilities, these never reach the variety and complexity of the human system (Postma et al., 2008). In our daily activities, spatial cognition is basic to most of our (mental) actions, i.e. when riding our bike or car to work, when playing ball sports, and when making difficult calculations. An important aspect of spatial cognition is spatial memory, that is, our ability to learn and remember what objects look like (recognition memory) as well as our ability to remember where objects are located (object location memory). Since these are both fundamental to all moving organisms it is not surprising that various mechanisms have evolved that allow us to identify objects, to remember the locations of several objects simultaneously, to find objects based on the locations of other objects, and to remember locations over time (MacDonald et al., 2004; Sluzenski et al., 2004). In the first place, these mechanisms consist of the processing of sensory information about the environment, which mostly includes visual information and movement information (i.e. proprioceptive information, vestibular signals reflecting accelerations of the head, and optic flow). The use of these information sources depends on the characteristics of the surrounding environment. That is, in a static environment we will mostly rely on visual information, whereas in a dynamic environment, visual as well as movement information are important. In addition, we may code this sensory information with respect to different reference frames. In this introduction, and in the other chapters of this thesis, we attempt to dissociate between the various reference frames used in static and dynamic environments in children and adults. We were specifically interested in children's ability to encode visual (and movement) information in order to recognize objects, to locate objects, and to navigate through the environment. The different studies presented in this thesis provide further insights in the question how children of primary school age (5 to 10 years) learn to deal with space?

1.2 Development of spatial cognition and spatial memory

Since spatial cognition is important for all higher cognitive functions in humans, knowledge of how this fundamental skill develops is central to our theoretical understanding of cognition in general (Newcombe & Huttenlocher, 2000). In the past century, three approaches regarding the development of spatial cognition have dominated the developmental literature (Sandberg et al., 1996). The first approach is from the well-known psychologist in the field of cognitive development: Jean Piaget (1896-1980), who became specifically known for his constructivist ideas, in which 'learning' from experiences plays a central role. In their book entitled "The child's conception of space", Piaget and Inhelder (1948) described in great detail which developmental stages children would go through while growing up.

They proposed that young infants think about spatial locations as having topological properties (i.e. separation, connectedness, continuity) and that, with age, children gradually learn to code objects' locations in projective space (i.e. order and amount) and Euclidean space (i.e. distances and angles). Thus, following the account of Piaget and Inhelder, many important spatial achievements are acquired relative late in childhood. In contrast, the second approach holds that mature spatial representations are already present at birth (Landau et al., 1981; Landau et al., 1984; Spelke & Newport, 1998). This approach suggests that spatial competencies present at birth are fundamental and subsequent environmental input is only enrichment, thus in a sense secondary to cognitive development. The third approach combines the former two approaches by stating that "biological preparedness interacts with the spatial environment that infants encounter after birth to create spatial development and mature spatial competence" (Newcombe & Huttenlocher, 2000). This latter approach claims to be an 'interactionist approach without being Piagetian', and seems to be most compatible with the results obtained in the field in the last decades.

We will start discussing children's ability to code visuo-spatial information, i.e. spatial relations within and between objects. Specifically, since the theory about how different spatial relations are coded and combined during the memory process (Huttenlocher et al., 1991) provides a good example of how different sources of information (e.g. visual and movement information) are currently thought to be combined in an optimal fashion in adults, but in a non-optimal way in children, denoting the developmental pattern observed in spatial memory. Hereafter we will discuss children's and adults' ability to represent spatial relations in combination with other spatial information sources (i.e. movement information) in different reference frames, and the different types of spatial coding which are dissociated in the literature based on these reference frames. Finally, we will briefly point out the neural substrates associated with these different types of spatial coding.

1.3 Spatial relations

The coding of sensory information (i.e. visual and/ or movement information) in a specific frame of reference is done at various grains of approximation and may be remembered with various degrees of certainty (Newcombe & Huttenlocher, 2000). Huttenlocher and colleagues (1991) proposed that the visual spatial relations within (i.e. object recognition) and between objects (i.e. object locations) are processed at mainly two levels of detail, which are hierarchically organized. They suggested that spatial information is stored at a fine-grained level (i.e. distance and direction) and a categorical level. Since fine-grained, metric information retrieved from memory comes with a degree of uncertainty, for example as is the case when retrieving a specific location of an object from memory, information is combined across hierarchical levels. As in Bayesian analysis, which uses prior knowledge to interpret new findings, inexact spatial information at a fine-grained level is combined, or 'weighted', with categorical information (Sandberg et al., 1996). Category information weights more, when uncertainty about the fine-grained information is greater, for example when the amount of time over which an object's location has to be remembered is greater. Although combining information at different levels of detail indeed approximates the correct location of an object, it also introduces a systematic bias. Huttenlocher and colleagues (1991) found that participants' reproduction of a dot's location drawn in a circle contained a bias toward the prototypical value (i.e. center) of a mentally imposed category, or, as shown in a more recent study (Plumert & Hund, 2001) category information can be represented by the associations among locations in a spatial configuration. Though, despite this systematic bias, integrating accumulating information seems to be highly adaptive, since it actually improves the overall accuracy of judgments by reducing the variability (Huttenlocher et al., 1991; Newcombe & Huttenlocher, 2000). Importantly, coding spatial information in our complex environment requires the combination of several sensory information sources. Huttenlocher and Newcombe (2000) suggested that the same basic principle that applied to this relatively simple ‘two-dimensional’ example in which only visual information is combined, will also apply to our natural environment. They recently introduced the ‘adaptive combination model’ (of which the above described hierarchical coding model is an example which can be applied to the modality of vision) in which, besides the certainty with which information is encoded (greater uncertainty associated with greater variance) (Huttenlocher et al., 1991), the salience of the information (i.e. amount of available information or feature types, like color, height, distinctiveness etc.), and children’s learning history affect the weights given to different sorts of spatial information (Newcombe & Ratliff, 2007). This would mean that different information sources (represented in different reference frames) are utilized to a certain degrees at varying points in development, depending on how the ‘priors’ influence the weighting of these information sources. The differential weighting is adaptive if it reflects developmental changes in the underlying reliabilities of the different information sources (Cheng et al., 2007), i.e. if development in the accuracy of using two information sources were uneven, it could be adaptive to weight one source more at an early age, and the other source more at a later age. We will come back to this model later in the introduction, but first we will show how an example of this model is applicable to studying children’s ability to code spatial relations within and between objects.

1.4 Development of spatial relations

The hierarchical dual coding model put forward by Huttenlocher and colleagues (1991), as discussed above, suggested that bias in locating objects toward a category prototype results from the use of categories to adjust inexactly remembered fine-grained information. In order to get a better understanding of its developmental origins, researchers from the same group investigated children’s hierarchical organization of space (Huttenlocher et al., 1994). Young children and adults searched for an object after they had seen it being buried in a rectangular sandbox. It was shown that children as young as 16 months of age searched close to the correct locations, suggesting that by this age, children are able to code location metrically along the single dimension of the rectangular sandbox. Furthermore, both children and adults demonstrated a, though different, pattern of bias, with 16-month-olds demonstrating a bias toward the centre of the sandbox, whereas 10-year-olds and adults mentally divided the box into two halves, with biases toward the centre of each half. This indicated that all age groups had combined fine-grained information with categorical information, but the different pattern of bias suggested that mental subdivision of single-dimensional space into multiple categories develops with age (Huttenlocher et al., 1994; Newcombe & Huttenlocher, 2000).

In a follow-up study the researchers also investigated children's hierarchical representation in a two-dimensional, instead of a one-dimensional, situation (Sandberg et al., 1996). They used the same stimulus set as in the 1991 study with adults (Huttenlocher et al., 1991), in which participants were asked to reproduce a dot's location drawn in a circle. In the adult study it was shown that the dot's location was metrically encoded along two dimensions by the participants; radial distance and angle. Furthermore, categorical bias effects were also obtained for these dimensions, with a radial distance bias toward a prototypical radial value of approximately 0.7, and an angular bias toward the 45 line of each quadrant mentally imposed on the circle. In the Sandberg et al. (1996) study it was investigated whether children 5 to 9 years also encoded metric fine-grained information in a two-dimensional space along two dimensions, and whether they showed patterns of bias similar to that of adults. It was shown that children are able to represent metric spatial information in two dimensions already at the age of 5 years. Also, 5-year-old children do construct spatial categories along the radial dimension of a circle, however, the construction of spatial categories along both radial distance and angle only emerges between the age of 7 and 9 years. An explanation for this later development can be found in the increment of dimensional processing capabilities: Sandberg (1999) showed that, even when horizontal and vertical axes, which divide the circle into quadrants, were perceptually available, 7-year-olds did not show the pattern of bias observed in older children and adults. It was therefore argued that "the acquisition of adult forms of spatial representation appears to be limited by encoding and/or processing capacities, rather than by spatial abilities" (Sandberg, 1999). In chapter 3 we investigated whether categorical and coordinate information would be weighted differently (and across different age groups) when the viewpoint on a visual scene including multiple objects changes. In addition to object location memory, the processing of spatial relations is also important for object recognition (see above). Therefore, in chapter 2 we tested children's ability to code categorical and coordinate spatial relations within (and between) objects.

1.5 Spatial reference frames

In order to process sensory information about the environment, i.e. representing spatial relations between and within objects, we use different reference frames. Without the use of a reference frame, we would not be able to describe and/or memorize the precise location (or orientation) of an object. In the spatial literature, a distinction is made between two particular frames of reference: the egocentric and the allocentric reference frame. In the egocentric frame of reference, locations of objects in space are represented with respect to one's own body (ego means 'self' in Greek), whereas in the allocentric reference frame, locations of objects are represented within an external framework, that is, in terms of distance and direction to the configuration of landmarks and/or the geometry of the environment (allo means 'other' in Greek). Although egocentric and allocentric reference frames rely on different mental processes (Parslow et al., 2004; Shelton & Gabrieli, 2004), the use of one does not exclude the use of the other. Several studies with rodents as well as with adults humans have shown that these frames of reference operate in parallel (Nadel & Hardt, 2004), possibly already at an early age (Nardini et al., 2006). That is, egocentric representations are considered specifically relevant for goal-directed motor actions, though, in case of movement over time, it would make sense if, in parallel to these egocentric representations, we would have a representation of our natural environment in which we could update our location, an allocentric representation. It has been suggested that, over the course of travel, egocentric representations are transformed into allocentric representations which are less prone to errors when distance (and time) over which is travelled increases, and this allocentric representation is kept ‘online’ in addition to the egocentric representation (Burgess, 2008; Byrne & Becker, 2008; Hartley et al., 2004; Milner et al., 1999; Nadel & Hardt, 2004). In contrast, in (short-term) learning paradigms, it might be the other way around, with (egocentric) habitual responses appearing slightly later in training than allocentric representations (Iaria et al., 2003; Packard & McGaugh, 1996).

Different types of spatial coding based on egocentric and allocentric reference frames (in static and dynamic environments) are dissociated. For the egocentric frame of reference, response learning (chapter 6 and 7) and egocentric spatial updating (or also called sequential egocentric strategy, Rondi-Reig et al., 2006, see chapter 5) are distinguished, with the former being specifically relevant in static environment and the latter in dynamic environments. Response learning is associative, and more limited in its usefulness than egocentric spatial updating (Packard & McGaugh, 1992, 1996; Tolman et al., 1946; White & McDonald, 2002). It refers to behavior that is directly guided by sensory information (e.g. when target location is visible), or which inflexibly employs a limited sequence of motor acts (i.e. one or two body turns, see Rondi-Reig et al., 2006) (Hartley et al., 2003; Iaria et al., 2003; Packard & McGaugh, 1996). Egocentric spatial updating, on the other hand, refers to our ability to update object’s locations relative to ourselves, coding distances and directions of our movements. Egocentric spatial updating, also called ‘dead reckoning’ (Newcombe & Huttenlocher, 2000), includes ‘path integration’, in which the movement from a specific start location is represented (Burgess, 2008; references). For the allocentric reference frame, place learning and allocentric spatial updating are dissociated, again with the former being relevant in static environments and the latter in dynamic environments (Packard & McGaugh, 1992, 1996; Tolman et al., 1946; White & McDonald, 2002). Place learning refers to our ability to use knowledge of the spatial relations between objects in the environment, for example when one needs to (re)locate an object. In addition, allocentric spatial updating is our ability to update our spatial location coding distances and directions from landmarks and/or geometry of the environment. That is, in allocentric spatial updating, the location of the participant is updated relative to the locations of objects in the environment, whereas in egocentric spatial updating object’s or start locations are updated relative to the participant (Burgess, 2008). It has been suggested that, during spatial updating continuous repetitions of translation between the egocentric and allocentric frames of reference take place (Byrne et al., 2007). An elegant way to experimentally dissociate the above described different types of egocentric and allocentric spatial coding is to test rodents and humans (children and adults) on their memory for object’s locations in real life (or virtual) mazes and/or in different types of object location memory tasks, i.e. tasks that manipulate the availability of the different reference frames.

1.6 Egocentric reference frame

It has long been held that, over the course of development, a shift would occur in using an egocentric to an allocentric reference frame (Huttenlocher & Presson, 1973; Piaget & Inhelder, 1948). However, over the years it became clear that these ‘early’ studies, had additional complications to their tasks, e.g. the type of response required (Huttenlocher & Presson, 1979; May, 2004), which made researchers conclude otherwise. Newcombe and Huttenlocher (2000) proposed that, instead of a qualitative shift in the use of certain reference frames, the observed developmental pattern actually reflects changes in the likelihood to use certain types of spatial coding based on the importance (or weights) attached to different information sources. This view on the development of spatial memory is in line with the adaptive combination model (Newcombe & Ratliff, 2007) discussed earlier in the introduction. In the literature it is now agreed that children are more ‘equipped’ than suggested by the early studies of Piaget. For example, response learning (goal-directed motor responses) is present early in life, not changing much over the course of development (Newcombe & Huttenlocher, 2000). In addition, the first signs of egocentric spatial updating are also observed at a young age. In order to discuss this literature, we will first explain the paradigm used to study egocentric spatial updating in adults. In the late nineties of last century, Simons and Wang (Simons & Wang, 1998), provided evidence for the use of egocentric spatial updating, by demonstrating that participants performed better on an object location memory task when, between presentation and test, the participant had moved him or herself to a new viewing position in the room compared to when the array of objects was rotated within the room over the same angle. Thus, participants preferred a change in view caused by their own movement over a view change caused by rotation of the array, although they provided the same visual information at test. Similar results have been obtained when participants were asked to imagine either themselves moving to a different location in space or rotating the array of objects over a similar angle (Wraga et al., 2000).

In order to investigate the use of different frames of reference in children 3-6 years, Nardini and colleagues (2006) adopted this spatial updating paradigm (Simons & Wang, 1998; Wang & Simons, 1999). Importantly, the child study obtained similar results as the adults studies, i.e. children preferred an array of objects to be consistent with the room over consistency with an egocentric representation. This effect was mainly due to their better performance on the condition in which a view change was caused by their own movement rather than by a rotation of the array. This finding could indicate that the ability to spatially update one’s position is already present early in life. Though, in both the child and adult study it was not investigated whether the advantage of own movement over array rotation was caused by participants’ use of landmarks for coding the locations of objects (allocentric reference frame) and/or whether it was caused by the fact that participants updated their position egocentrically. In a follow-up study with adults, Burgess and colleagues (2004) demonstrated that varying the array’s consistency with an external landmark, affected participants’ performance. They therefore concluded that the ability to use distal landmarks and egocentric spatial updating (movement cues) for coding location exist in parallel to the use of purely egocentric representations of location.

Newcombe and colleagues (1998) provided an answer to the question whether, children can also combine distal landmarks and movement cues when walking to a different position in a room before relocating an object. As a follow-up on the experiments investigating children’s hierarchical organization of a one dimensional space (Huttenlocher et al., 1994), which we discussed earlier, Newcombe and colleagues (1998) employed this paradigm to examine children’s use of different frames of reference. The researchers showed that children 16-36 months of age were able to correctly search for hidden toys in a long rectangular sandbox after, between presentation and test, having walked to the opposite side of the sandbox. Moreover, it was demonstrated that children of all ages performed above chance level when the distal landmarks were not available in the testing room, and children older than 22 months of age increased performance when the distal landmarks were available compared to when this was not the case. These latter findings indicated that indeed, at already a young age, children used landmarks in parallel with movement cues for coding location.

While the use of an egocentric reference frames (i.e. response learning and egocentric spatial updating) is not changing much with development, it has been shown that the use of an allocentric frame of reference (e.g. place learning) continues to change over the years (see chapter 6). The study of Newcombe and colleagues (1998) showed that the first signs of place learning, i.e. the ability to use knowledge of the spatial relations between objects in the environment, is already observed in children 22 months of age, in addition, a different set of studies demonstrated that this ability develops well into primary school age, up until the age of 5 to 7 years (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003; Overman et al., 1996). The studies referred to were based on paradigms initially designed to test place learning in rodents (Morris, 1981; Tolman et al., 1946), and were adapted to also probe the use of an allocentric reference frame in children and adults. In chapter 6, we studied the extent to which the developmental trajectory of response learning and place learning depends on an increment of relevant experience.

1.7 Allocentric reference frame

A task widely used to study place learning in rodents is the Morris water maze (Hamilton et al, 2007; 2008; Maurer & Derivaz, 2000; Morris, 1982; Pearce et al., 1998). This task consists of a large circular pool in which rats are required to escape from the (opaque) water by swimming to a platform hidden just under the surface. During testing, the platform remains in the same spatial location, while, on each trial, the animal is led into the water in a different start location. For this reason, simple motor responses (i.e. response learning) are ineffective, thus the animal learns to locate the platform using the configuration of distal landmarks. In a recent study, Hamilton and colleagues (2007) contrasted place learning and directional responding in the Morris water maze by repositioning the pool in the room so that the absolute spatial location of the platform (in relation to the distal landmarks in the testing room) was centered in the opposite quadrant of the pool. In line with the expectations of the researchers, the rats were searching for the platform in the relative ('new') location rather than in the absolute location in space, suggesting that, in the traditional Morris water maze, directional responding predominates over navigating to a precise spatial location. Interestingly, in a follow-up study (Hamilton et al. 2008) it was shown that, when the pool was filled up with water, such that the pool wall was nearly invisible, rats showed a preference for place navigation over directional responding. Thus, it seemed that the pool wall influenced whether the distal landmarks provide directional or place cues. The researchers suggested that a reduction in the salience of the pool wall might have increased the salience of the distal cues. This is an interesting suggestion worth of further investigation.

In two chapters of this thesis, we investigated place learning (chapter 6) and boundary-related learning (i.e. directional responding, chapter 7) in children. To our knowledge, the only study that actually investigated children's ability to show boundary (or wall) related learning in a paradigm similar to that of the Morris water maze, is the one presented in chapter 7. It was shown that 5 and 7-year-old children were able to use distal orientation cues in addition to information provided by the boundary of the enclosed environment. This finding is consistent with the extensive literature on children's ability to reorient in an enclosed environment. These studies all used a typical orientation paradigm, in which an object is hidden in the corner of a rectangular room of which one of its walls is painted in a distinctive color (see Cheng & Newcombe, 2005 for a review). Although the surface geometry alone does not have a direct role in representing an object's location, in combination with landmark information it does. Thus, it was reasoned that, in case children would not use the colored wall, they would search in the two geometrically equivalent corners of the rectangular room. Three previous studies have shown that, when 20-month-old children were tested in a small testing room (4 by 6 feet) they ignored the distinctive colored wall, performing at chance level in the two geometrically correct corners (Hermer & Spelke, 1994; 1996), and only 5 and 6-year-old children were able solve the task (Hermer-Vazquez et al., 2001). However, in case children of different ages were tested in a large testing room (8 by 12 feet), they performed correctly on the search task, thus combining geometric with landmark information (Learmonth et al., 2002; Learmonth et al., 2001) at already 18 months. It was proposed that the ability of older children to solve the task, stemmed from the employment of spatial language (Hermer-Vazquez et al., 2001; Hermer-Vazquez et al., 1999). However, the observation that rhesus monkeys (Gouteaux et al., 2001) were also able to correctly solve similar tasks, together with the fact that verbal interference effects were not replicated (Ratliff & Newcombe, 2005; Ratliff & Newcombe, 2008), limits the viability of this hypothesis.

An alternative explanation for the findings could be offered by the adaptive combination model, which, as discussed before, states that different sources of (environmental) information (geometry and landmarks) are weighted differently in different situations, depending on factors such as the certainty with which the information sources are encoded, their salience and perceived usefulness (Learmonth et al., 2008; Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007). The adaptive combination model is considered the 'overall family' of different approaches to estimation tasks (Newcombe & Ratliff, 2007), as for example the hierarchical coding model of Huttenlocher and colleagues (1991), in which, as already discussed in great detail at the beginning of this introduction, visuo-spatial relations are thought to be processed at different levels of detail. Another example, one of specific interest in relation to the studies just discussed, is the 'boundary proximity model' by Hartley and colleagues (2004). This model proposes an abstract representation of the proximity of a location to the walls of an enclosed environment. When remembering a location in an enclosed environment (i.e. a rectangular enclosure), two distances are encoded, the absolute distance from a wall and the relative distance (ratio of distances to different walls). The absolute distance weights more in an estimation of location when the location (of oneself or an object) is close to a wall, and the relative distance is weighted more when the walls are distant. Notably, this abstract representation seems consistent with the neural coding of a location by the firing of place cells in the hippocampus (Ekstrom et al., 2003; Morris et al., 1982; O'Keefe, 1976; Ono et al., 1991; Packard & McGaugh, 1996; Pearce et al., 1998). In addition, the distal landmarks provide orientation and is most likely maintained by the system of head-direction cells (Taube, 1998, see also Burgess, 2008). In chapter 4 of this thesis we investigated children's combined use of different types of spatial information to locate objects in the environment. In addition to the literature on children's ability to reorient in an enclosed environment (Learmonth et al., 2001; Cheng & Newcombe, 2005), we were interested in children's ability to update their spatial location (and the location of the to-be-relocated-object), coding distances and direction from (local or distal) landmarks in the environment (i.e. allocentric spatial updating).

Thus, as supported by the results obtained in the Morris water maze studies (Hamilton et al, 2007; 2008) and the studies which used a reorientation paradigm, learning a location in a bounded environment depends on the absolute and relative distances from wall(s), and from distal landmarks which provide orientation. The adaptive combination model proposed that the information sources are differently weighted in different situations, and are changing with development. This will also hold for navigation behavior, when movement over time plays a significant role. In chapter 5 we tested children on a navigation task, in which 'geometry' did not play a significant role, however, the use of body movement cues (optic flow) (egocentric spatial updating) was compared with the use of distal landmarks (allocentric spatial updating), while learning a route.

1.8 Neuroanatomical substrates

Through neurophysiological studies with rodents (i.e. single cell recordings) (Ono et al., 1993; O'Keefe & Speakman, 1987; O'Keefe, 1976; O'Keefe & Dostrovsky, 1971), neuropsychological studies with patients (Bohbot et al., 1998; Maguire et al., 1998; Maguire et al., 1996; Maguire et al., 1997; Van Asselen & Postma, 2008), and imaging studies with healthy adult humans (Doeller et al., 2008; Iaria et al., 2003), different areas in the brain have been associated with specific spatial behaviors. From a fundamental point of view, this is interesting, since it gives the possibility to link behavioral developmental patterns to the maturation of these brain areas during childhood.

To start with the neural substrates involved in the processing of spatial relations, it has been suggested that the right cerebral hemisphere processes coordinate spatial relations more effectively and the left cerebral hemisphere is specialized in processing categorical spatial relations (Kosslyn, 1987). However, the evidence for a hemispheric specialization in the processing of spatial relations is inconclusive. Although an advantage for the right hemisphere in encoding coordinate relations is often shown, the hypothesized left hemispheric specialization for categorical spatial relations appears weaker (Banich & Federmeier, 1999; Dépy et al., 1998; Koenig et al., 1990; Hellige et al., 1994; Hellige & Michimata, 1989; Kosslyn et al., 1989, 1992, 1995; Laeng, 1994; Laeng & Peters, 1995; Laeng et al., 1999; Michimata, 1997; Parrot et al., 1999; Rybash & Hoyer, 1992), and even opposite results have been obtained (Niebauer, 2001; Sergent, 1991). It was suggested that these differences in findings might be attributed the different methodological set-ups of the tasks (Bruyer et al., 1997; Wilkinson & Donnelly, 1999). In chapter 2 we investigated whether children's ability to code categorical and coordinate spatial relations within and between objects develops with age, and if so whether corresponding changes in hemispheric specialization can be observed.

The processing of sensory information about the environment in different frames of reference, have also been linked to different neural structures. We already mentioned the firing of place cells in the hippocampus for encoding location to extended boundaries. In addition, the striatum seems to be involved in navigation towards a location marked by a distinct visible landmark (response learning). In both cases the head-direction system is required to provide orientation with the use of distal landmarks (O'Keefe & Nadel, 1978; Packard & McGaugh, 1996; Poldrack et al., 2001; Doeller and Burgess, 2008). Up to this point no direct evidence for neural structures associated with the use of different reference frames exists for children. However, a developmental dissociation of response and place learning supports the theory that the two related neural systems develop at different rates, with an early development of striatal function, and a delayed maturation of hippocampal function (Bachevalier & Beauregard, 1993; Dumas, 2005; Stanton, 2000). Thus, the marked improvement in place learning during primary school, might reflect an important developmental time-period for maturational changes in the hippocampus (Newcombe & Huttenlocher, 2000; Overman et al., 1996).

Importantly, it should be noted that experience does stimulate brain development (Greenough et al., 1987 and Shonkoff & Philips, 2000 in Newcombe et al., 2007). Therefore, developmental changes in spatial behavior might depend on a combination of biological maturation, on experience with certain information sources, and/or on their (possibly bi-directional) interaction (Newcombe et al., 1998). Imaging studies with children or studies with children from clinical populations might provide further insight in the respective roles of brain maturation and/or experience in developmental changes (Overman et al., 1996).

CHAPTER 2

THE DEVELOPMENT OF CATEGORICAL AND COORDINATE SPATIAL RELATIONS

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Abstract

Two classes of spatial relations can be distinguished in between and within object representations. Kosslyn (1987) suggested that the right hemisphere (RH) is specialized for processing coordinate (metric) spatial information and the left hemisphere (LH) processes categorical (abstract) information more effectively. The present study examined the developmental pattern of spatial relation processing in 6-8 year olds, 10-12 year olds and adults. Using signal detection analyses we calculated sensitivity and bias scores for all age groups. The results indicated that older children and adults showed a greater response bias than younger children. Also, discrimination sensitivity for spatial relation changes clearly improved with age. For the oldest children (10-12 year olds) and adults this improvement was accompanied by a RH specialization. In contrast with Kosslyn's claim, this RH advantage also applied to the processing of categorical spatial information. The results are discussed in terms of a right hemispheric specialization for spatial relation processing which matures with age.

2.1 Introduction

The visual processing of spatial relations between objects and the relations between features within objects enables us to identify objects, to guide actions and navigate through our complex environment. Two general classes of spatial relations between objects or within single objects are assumed to exist (Kosslyn, 1987; Kosslyn et al., 1989). The so called *coordinate* relations offer fine-grained and subtle metric descriptions of the visual world, necessary to guide precise movements. In contrast, c*ategorical* spatial relations afford invariant abstract spatial relations useful for viewpoint independent object recognition and prototypical spatial location coding (Kosslyn et al., 1987; Jager & Postma, 2003). Kosslyn (1987) hypothesized that both forms of spatial relations are processed through distinct hemispheric networks. He suggested that the right cerebral hemisphere (RH) processes coordinate spatial relations more effectively and the left cerebral hemisphere (LH) is specialized in processing categorical spatial relations. Subsequently, a number of studies concentrating on different functional domains (perception, action, imagery, verbal communication, working and long-term memory) and using different methodological set-ups (visual half field studies, computer simulations, patient lesions and brain imaging studies), task qualities (task difficulty, response mode, practice and feedback), stimuli features (display features and exposure duration) and subject characteristics (gender and handedness) has investigated this dichotomy (Haun et al., 2005; Huttenlocher et al., 1991; Jager & Postma, 2003; Wang, 2004). Thus far, most studies indeed reported an advantage for the RH in encoding coordinate relations. However, the hypothesized LH specialization for processing categorical information appears weaker (Banich & Federmeier, 1999; Dépy et al., 1998; Koenig et al., 1990; Hellige et al., 1994; Hellige & Michimata, 1989; Kosslyn et al., 1989, 1992, 1995; Laeng, 1994; Laeng & Peters, 1995; Laeng et al., 1999; Michimata, 1997; Parrot et al., 1999; Rybash & Hoyer, 1992).

An interesting question arises as to how the processing of categorical and coordinate spatial information and corresponding hemispheric preferences change with age. Huttenlocher and colleagues (1991) asked children and adults to search for hidden toys in a rectangular sandbox. They proposed a hierarchical dual coding system, in which coordinate spatial information is weighted with general categorical information. While coordinate information alone will normally suffice to retrieve any hidden target, categorical information alone is ineffective. Thus, in order to reduce cognitive load and in such way effectively remember an object's location, fine-grained and categorical information need to be combined, 'hierarchical coding'. In the study of Huttenlocher and colleagues (1994), it was shown that children as young as 16 months of age are capable of selecting the correct locations. Even more interesting, however, was the finding that the children showed a pattern of bias towards a category prototype, indicating the combined usage of categorical and coordinate information is already present at this early age. Though, since this pattern of bias did not (yet) correspond to a mature representation, it was suggested that the ability to process both exact, coordinate information and categorical spatial relations between objects in order to establish subjective categories seems to systematically improve with age (Huttenlocher et al., 1994; Newcombe & Huttenlocher, 2000).

Related to the question whether and how processing of different types of spatial relations develop with age, there is the intriguing issue of concomitant changes in hemispheric specialization. To our knowledge, up to this point only two developmental neurocognitive studies actually did examine age differences in processing the distinct forms of spatial relations (Koenig et al., 1990; Reese & Stiles, 2005). However, these studies have yielded inconsistent findings. Koenig and colleagues (1990) concluded that children as young as 5 years of age show hemispheric processing differences. On the contrary, Reese and Stiles indicated that, testing children of 8 years and older, hemispheric specialization only appears at the age of 10. A possible explanation for this difference in findings is that the cognitive domains under study were not the same; Koenig et al. (1990) focused on the perceptual encoding of spatial relations whereas Reese and Stiles (2005) were more interested in the developmental pattern of spatial relations in visual mental imagery.

In light of the foregoing, the aim of the present study was to gain more insight in the developmental changes in processing of categorical and coordinate spatial relations and the corresponding changes in hemispheric specialization. Hence we tested three age groups (6-8 years, 10-12 years, and 18-25 years) on a spatial relation change detection task. In this computerized divided-visual-field task, children and adults had to decide whether animal line drawings did or did not change. In case the drawings did change, they either changed in a categorical or a coordinate manner. This paradigm is similar to the ‘identity test’ developed by Laeng (1994), and is specifically suitable for research with children. Postma and Laeng (2006) pointed out that the exact hemispheric engagement in spatial relation processing might differ across perceptual, memory, imagery or constructive cognitive domains. We studied spatial relation processing in a combination cognitive domains, namely in a perceptual working memory situation. While a general progress with age in spatial relation processing can be expected, it was of particular interest to see whether the two classes of spatial relations differed herein, and whether concomitant changes in hemispheric involvement were present. Moreover since the current change detection task afforded a signal detection approach, we could establish to what extent cognitive development comprises sensitivity and bias changes. This is specifically interesting since previous research has shown that participant’s sensitivity and bias scores on recognition memory tasks are, to a certain extent, correlated with age and hemisphere (Berch and Evans, 1973; Glosser et al., 1998; Windmann et al., 2002a; Windmann et al., 2002b). For example, older children were shown to exhibit a greater response biases (Berch and Evans, 1973) and a more liberal response bias was reported for visuo-spatial information encoded by the RH (Glosser et al., 1998).

2.2 Method

2.2.1.Participants

Hundred-twenty right-handed participants (80 children and 40 students) were included in the study. The children were divided in two groups defined by age: 6-8 year olds (mean age = 7.3, *SD* = 1.15) and 10-12 year olds (mean age = 11.4, *SD* = .84). The youngest age group included an equal number of boys and girls. The older age group consisted of 18 girls and 22 boys. All children were recruited from a local elementary school and their primary caregiver gave consent for participation. The students (mean age = 22.2, *SD* = 3.29) were recruited through advertisements at Utrecht University. They either received credit points or a small amount of money for participating. All adult participants gave written consent for participating in the study. Again equal numbers of males and females participated. All children and adults reported to be healthy, had normal or corrected to normal vision and were unaware of the rationale of the experiment.

2.2.2. Design

To assess possible age differences in hemispheric specialization for processing spatial relations, a task of the matching to sample kind was used. This 'memory' task prohibited the participants to use other perceptual cues (e.g., contour differences), or to develop strategies (e.g., comparing patterns of eye movements when visually inspecting the stimuli) that may lead to the recognition of differences in the stimuli (Laeng, 1994). The task was similar to a paradigm first developed by Laeng and his colleagues (Laeng, 1994; Laeng & Peters, 1995: Laeng et al., 1999). Participants needed to decide whether animal line drawings did or did not change. In successive order, a reference drawing and a test drawing were presented on the computer screen and the subject was asked to assess whether the test drawing was the same or different compared to the reference drawing. On half of the trials subjects needed to respond 'same' and on the other half 'different'. In half of the 'different' trials a categorical transformation (i.e. laterality change) was involved and the other half consisted of a coordinate transformation (i.e. size or distance). The categorical and coordinate changes used in the task are illustrated in Fig. 1. These test stimuli manipulations were previously successfully used by Laeng and Peters (1995).

2.2.3. Procedure

The task was presented on a high-resolution 15-inch computer. Participants were seated approximately 52cm from the computer screen and were asked to rest their head on a chin pole, which was aligned with the centre of the computer screen. Every participant first received a practice block and thereafter two blocks of 80 testing trials. In each test block a total of 20 categorical changes and 20 coordinate changes were included. The regular size of each drawing used in the study was 4 cm by 3.5 cm and in case a coordinate change had taken place for the single animal pictures the size of the drawing was 2.7 cm by 2.3 cm. When two animals were presented the distance between the figures was 2 mm and in case of a coordinate change 3.2 cm.

An experimental trial consisted of five consecutive displays: First, a central red fixation point appeared for 500 ms on the screen to indicate the beginning of the trial. Second, a cue (or reference drawing), consisting of a black-and-white drawing of one or two animal(s), was presented in the centre of the screen for 750 ms. Both one and two animal(s) pictures were used in order to guarantee the generalizability of spatial relation processing to spatial relations between objects and between features within objects. In case two animals were shown, these were placed right beside (horizontally) or above (vertically) each other. Third, again for 500 ms a central fixation point appeared, but this time in black to signify the transition from reference to test stimulus. Next, the test drawing, which was the same or categorically or coordinately different, was shown for 100 ms in either the left visual field (LVF) or in the right visual field (RVF). The test drawing appeared at 1.1º – 13.5º (N.B. range is caused by differences in presentation of reference and test drawings, Figure 1) from the fixation point. An equal number of test stimuli appearances in either visual field were randomized across trials. Finally, a blank screen appeared until the subject decided whether the test drawing was the same or different compared to the reference drawing previously presented. After the subject made a decision by pressing either a green ('same') button or a red ('different') button, the trial was terminated. The assignment of 'same' and 'different' buttons to both hands was counterbalanced across participants.

Before the test trials were administered, together with the experimenter, the participants read the instruction for the task from the computer screen. After the subjects indicated that they had understood the instructions, they were familiarized with the reference and test drawings and the possible categorical or coordinate changes. The subjects completed eight different practice trials in which they were specifically asked to keep focused at the little star in the middle of the computer screen. During these practice trials participants received feedback about their performance, while during the actual test trials this was not the case. After practice, participants were told that they would receive the test stimuli, and that these would go faster than the ones in the practice trials. Again it was pointed out that they needed to attend to the fixation point in the middle of the computer screen. After participants received the two test blocks, they were told that they did do well and were thanked for participation. Total testing time took about 10 minutes.

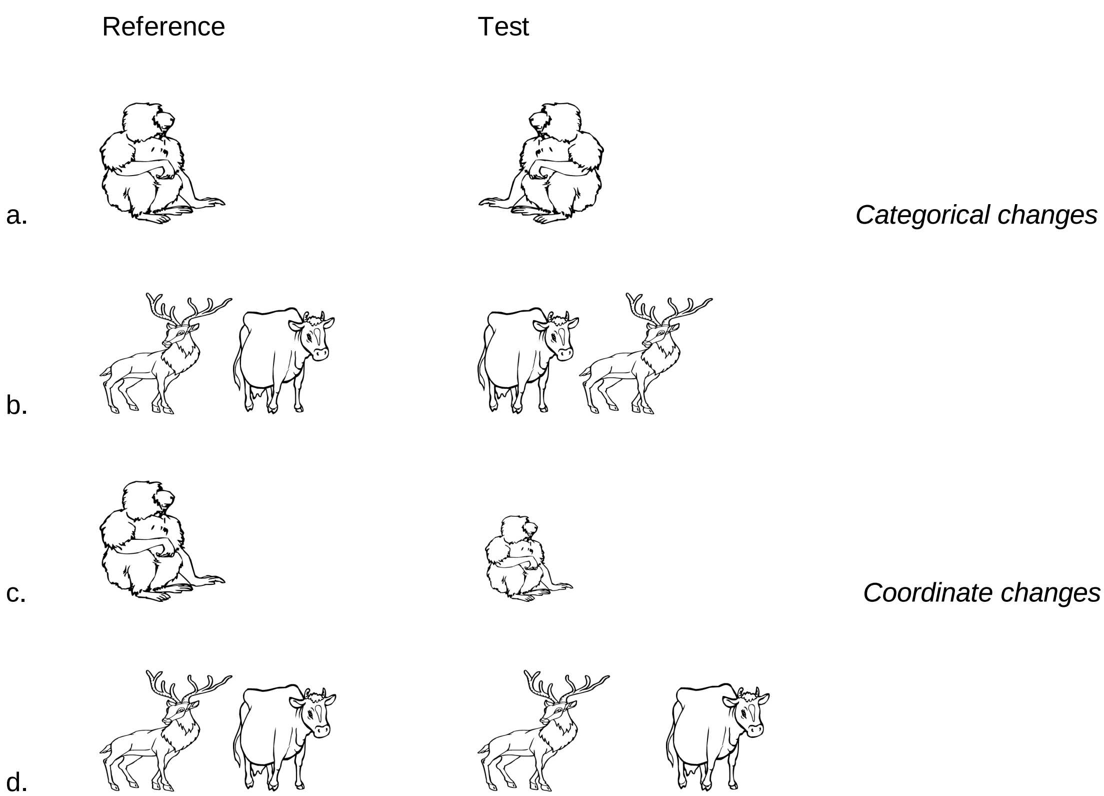


Fig. 1. Reference and test stimuli for categorical (a & b) and coordinate (c & d) changes.

2.3 Results

Percentage of errors and reaction times (RTs; i.e. time between presentation of test stimulus and the actual response in milliseconds) were registered. For all three groups, RTs and error percentages were positively correlated, indicating no speed-accuracy trade off. However, since error percentages were relatively high for both the categorical and coordinate trials (especially for the youngest age group), not enough data was available for the reaction time analysis since only the correct RTs should be included. Therefore, we chose to limit our analyses to error rates rather than RTs. In order to derive a measurement for recognition memory, sensitivity (Pr) and response bias (Br) were calculated using a two-high-threshold model underlying Signal Detection Theory. The sensitivity (also called memory discrimination) refers to the accuracy of memory and represents the proportion that participants are certain in deciding whether or not an item was previously presented. The response bias refers to the strategy that is adopted (that is, saying ‘seen before’) when participants are uncertain about whether or not they had seen the item before (Glosser et al., 1998; Windmann et al., 2002a; Windmann et al., 2002b). At a behavioral level, these measurements are largely independent from one another (Snodgrass & Corwin, 1988). Participants performance was summarized by the following two measures: the hit rate (H), which is the probability that the participant correctly responded that test and reference drawing were the same and the false alarm (FA) rate, the probability that the participant incorrectly classified the drawings as same while they were actually different[1]. With the purpose of computing participants’ sensitivity and bias scores the following formulae were used: Pr = H – FA and Br = FA/ (1-Pr) (Snodgrass & Corwin, 1988). To eliminate hit rates of 1.0 and FA rates of 0, the overall hit and FA rates were corrected by adding .5 and divided by N + 1, in which N corresponds to the number of same and different items. Both sensitivity and bias scores ranged from nearly 0 to almost 1.0. In Table 1 mean proportion of respectively hit, FA, sensitivity and bias scores are shown for all age groups. In the following section, sensitivity scores, bias scores, hit rates and FAs are subjected to different analyses.

2.3.1. Sensitivity

First, the overall sensitivity scores were subjected to a repeated measure ANOVA with Group (3) as between-subjects factor and Hemisphere (2) as the within-subject factor. The analysis revealed a significant difference between age groups, F (2, 117) = 56.61 p < .001, indicating that participants become more sensitive to the spatial changes with age. Post hoc comparisons showed that the 10-12 year olds (Pr = .64) and the adults (Pr = .71) did not differ from each other in sensitivity (p = .094), but that they were significantly more sensitive to the spatial transformations than the 6-8 year olds (Pr = .37). Additionally, the Hemisphere main effect also reached significance, F (1, 117) = 5.92 p < .05. This effect indicated that participants were more sensitive to spatial transformations presented to the

[1] We thank one of our reviewers for his/her comment that in the classic perceptual signal detection situations, a false alarm means incorrectly detecting of a change. On the contrary, we adopted the approach that is often used in the memory domain, in which the hit rate corresponds to the probability that the subject classifies an old item as old, and the false alarm rate corresponds to the probability that the subject classifies a new item as old (Snodgrass & Corwin, 1988). It is for this reason that we labelled a (categorical or coordinate) change, which can be considered comparable to the new items in the original recognition memory tests, a False Alarm.

LVF/RH than presented to the RVF/LH. This latter effect interacted significantly with the factor Group, F (2, 117) = 4.57 $p < .05$. A paired-samples T test showed that for the youngest age group (6-8 years) there was no hemispheric difference in sensitivity, t (39) = -.80, $p > .05$, whereas there was for the older children (10-12 years) and adults, respectively t (39) = 2.52, $p < .05$ and t (39) = 4.0, $p < .001$.

2.3.2. Bias

Beside the sensitivity age effects, groups did also differ from one another in their bias measure (Br), F (2, 117) = 4.63 $p > .05$. A post hoc test (Bonferroni corrected) revealed that, when uncertain about the similarity of the stimuli, the children as well as the adults showed a moderate response bias in responding ‘same’ more than ‘different’. This tendency was stronger for the older children (.75) and adults (.76) than for the youngest age group (.68). Also, a main effect was found for the factor Hemisphere, F (1, 117) = 33.21, $p < .001$. That is, overall participants showed a smaller response bias for the test stimuli presented to the LVF/RH (.71) compared to the RVF/LH (.75).

2.3.3. Hit rates

The third ANOVA performed on the hit rates did not show any significant effects, that is no hemisphere and age effects were found for the amount of reported hits.

2.3.4. Categorical and Coordinate Changes (FAs)

Since hit rates cannot be broken down in categorical and coordinate spatial changes as these only include the probability that the participant correctly responded that test and reference drawing were the same, the factor Type of Spatial Change (categorical and coordinate) could not be added as a factor to the sensitivity and bias analyses. However, in order to gain further insight in how the above mentioned developmental changes stretch out to the class of categorical and coordinate spatial relations, the trials on which indeed a change had taken place were analysed further. Errors on these trials corresponded to what above has been labelled as false alarms (FAs). The effects which include the Type of Spatial Change (2) factor will be outlined below. The reported false alarm rates differed significantly between both spatial transformations (F (1, 117) = 581.11 $p < .001$) showing that, overall, participants recognized the coordinate spatial changes better than the categorical changes. Type of Spatial Change interacted with Group, F (2,117) = 8.37, $p < .001$, indicating that while the younger children produced more FAs than the older age groups, they especially did so for the coordinate spatial changes (Fcoo (2,117) = 44.45 $p < .001$; Fcat (2,117) = 24.41 $p < .001$). Furthermore, a two-way interaction effect of Type of Spatial Change by Hemisphere, F (1, 117) = 29.82, $p < .001$ was obtained as well as an higher order interaction of Type of Spatial Change, Hemisphere and age Group, F (2, 117) = 4.61, $p < .05$. These effects showed no hemisphere effect for the coordinate task condition ($p > .05$), but for the categorical task the overall false alarm rate was significantly higher for the items presented to the LH than to the RH. The latter, and to our opinion most interesting, result that emerged from this analysis (plotted in Fig. 2.) showed that it concerned the older children (10-12 years, t (39) = 6.38, p < .001) and adults (t (39) = 7.04, p < 001), but not the younger children (6-8 years), t (39) = .55, p = .584.

Table 1

Descriptive statistics of participants performance on the spatial relation change detection task

Group	H	LH/RH	FA (cat/coo)	LH/RH	Pr	LH/RH	Br	LH/RH
6-8 yrs	.78 [.14]	.79/.77	.42 [.13] (.53/.30)	.42/.41	.37 [.22]	.37/.36	.68 [.13]	.70/.66
10-12 yrs	.90 [.08]	.90/.90	.27 [.07] (.43/.09)	.29/.24	.64 [.13]	.62/.65	.75 [.13]	.77/.73
18-25 yrs	.92 [.06]	.93/.92	.22 [.04] (.39/.03)	.25/.19	.71 [.07]	.68/.73	.76 [.13]	.79/.72

H = hit rate [SD]; FA = false alarm rate [SD] (cat/coo); Pr = sensitivity score (H-FA) [SD]; Br = bias score [FA/(1-Pr)] [SD]; LH/RH = left hemisphere/right hemisphere

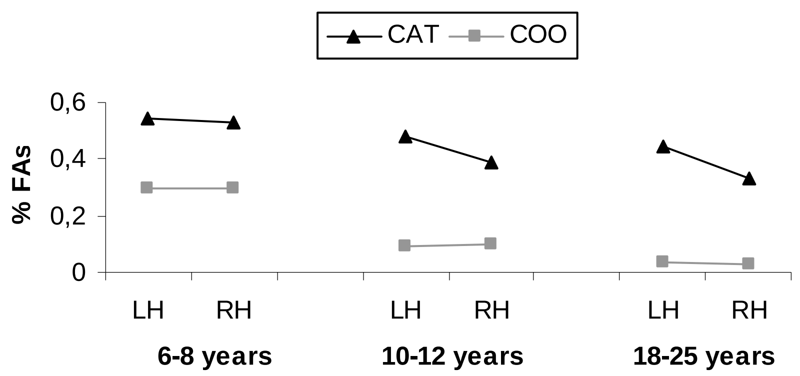


Figure 2. Percentages FAs for the categorical and coordinate changes presented to the LVF/RH and to the RVF/LH for each age group separately.

2.4 Discussion

The present study examined developmental changes in processing categorical and coordinate spatial relations and corresponding (changes in) hemispheric specialization. We compared 6-8 year olds, 10-12 year olds and adults in their overall performance on a computerized spatial relation change detection task, in which categorical and coordinate object relations were assessed. Using signal detection analyses we calculated sensitivity and bias scores for all age groups.

Importantly, it was shown that discrimination sensitivity for spatial relation changes clearly improves with age: 10-12 year olds and adults detected spatial transformations better than the 6-8 year olds. This finding is in line with earlier research addressing categorical and coordinate spatial relation processing in different age groups (Huttenlocher et al., 1994; Newcombe & Huttenlocher, 2000). More specifically, we observed that this sensitivity group effect interacted with the visual field (i.e. hemisphere) in which the test stimulus was presented. The older children (10-12 years) and adults, in contrast to the youngest age group (6-8 years), showed an advantage for the RH in processing spatial relations. The adult RH advantage for perceiving spatial transformations in general (thus averaged over both categorical and coordinate changes) and the lack of such an overall laterality effect in young children (5 and 7 years old) corroborates and extends previous studies (Koenig et al., 1990; Laeng, 1999; Rybash & Hoyer, 1992; Sergent, 1991). Reese and Stiles (2005) found older children (8 and 10 years old), comparable to adults, to perform more accurately on the trials presented to the LVF/RH. These results together with our findings might suggest that an overall RH advantage for processing spatial relations emerges between 8 to 10 years and seems almost complete after age 10, since the older children in our study did not differ from the adults in general sensitivity nor in recruitment of specific hemispheric resources (i.e. the RH).

Beside discrimination sensitivity, an age difference was found for the response bias. All participants had the tendency to say ‘same’ more often than ‘different’. However, this effect was stronger for the older children and adults than the youngest age group. Different reasons could account for this finding. For example, affective, contextual or executive factors all contribute to making decisions in uncertain situations and might have a differential impact on different stages in development (Glosser et al., 1998). A plausible explanation, related to the executive factors mentioned, might be sought in the maturity of the frontal regions of the brain during development. Windmann and colleagues (2002b) proposed that response bias is a top-down controlled process, mediated by prefrontal areas. Consequently, the maturation of these areas might cause younger children to differently respond in the face of uncertainty. In addition, the RH showed a smaller response bias than the LH. Laterality effects for response bias have been reported before and retraced to the early organization of the visual system (Glosser et al., 1998). It should be acknowledged that Glosser and colleagues (1998) for a different task obtained slightly different hemispheric bias trends. Future research should more thoroughly examine the function of age (and related to this the development of the prefrontal cortex) and hemispheric processing differences in the use of strategies in uncertain circumstances.

More specific insights in the development of processing categorical and coordinate spatial information derived from analyzing the type of errors when producing a FA (i.e. the probability that the participant incorrectly missed a categorical or coordinate change). The results indicated that all participants performed very poorly on the categorical trials. In order to correctly solve these trials, participants needed to assign an invariant abstract spatial label to describe the relation between the depicted animals (Laeng, 1994; Laeng & Peters, 1995: Laeng et al., 1999). It has been reasoned before that the LH specialization for language processing is related to its preference for categorical spatial relation processing (Kosslyn, 1987; but also Parrot et al., 1999). Noticeably, in many circumstances, participants might use a verbalization strategy for representing categorical spatial relations. However, the categorical changes used in our task appeared to be quite difficult (possibly due to the limited presentation time of the stimulus), thus preventing effective employment of such a verbalization strategy. Consequently, participants might have chosen instead to focus on the (metric) details in or the global contour of the pictures presented (instead of identifying the animals and their laterality), and in such way applying a coordinate strategy. Converging evidence for this suggestion is offered by the corresponding hemisphere effects. That is, the older children (10-12 years) and adults made fewer ‘categorical’ FAs in the RH. The younger children (6-8 years), in contrast, did not show a successful right hemispheric strategy for processing these spatial relations. The fact that Laeng and Peters (1995) did find a LH effect using similar categorical stimuli might indeed be sought in time of presentation. In their task, the stimuli appeared one and a half times longer (150 ms) on the computer screen, giving the participants the opportunity to more easily identify the (relation between) the depicted animals.

In conclusion, the present study showed that young children process spatial relation information in a qualitatively different way than older children. First, children become more sensitive to spatial changes with age. Second, this improvement was accompanied by a hemispheric specialization, namely an increased RH efficiency. Third, older children and adults showed a differential response bias, possibly showing a greater involvement of the prefrontal cortex. Fourth, with respect to functional lateralization, Kosslyn’s (1987) claim that categorical and coordinate spatial information are processed by the LH and RH respectively was not replicated in this study. On the contrary, the older children and adults showed a RH advantage for processing categorical spatial information. We speculate that this advantage might be caused by the difficulty of the categorical transformations used in this study. Because of limited presentation time, participants might have made a coordinate decision on these trials instead of using a categorical strategy. Future research will have to extend these results to other cognitive domains in which spatial relation processing is relevant, such as (delayed) memory and spatial language usage (Bowerman, 1996; Kemmerer, 2006; Postma et al., 2006; Postma & Laeng, 2006).

CHAPTER 3

CHILDREN'S USE OF SPATIAL REFERENCE FRAMES AND SPATIAL RELATIONS IN A SCENE RECOGNITION TASK

Bullens, J., Van der Ham, I.J.M., De Goede, M. & Postma, A. Children' s use of spatial reference frames and spatial relations in a scene recognition task. (*submitted for publication*)

Abstract

In order to represent spatial relations between objects in a scene we may adopt different reference frames: a visual snapshot (‘integrated picture’), an egocentric (body-referenced) and/or an allocentric (external-referenced) reference frame. These reference frames rely upon different neural structures. Children use different frames of reference more effectively with age, possibly showing the functional maturation of these neural structures. In the present study, children 5 to 10 years were tested on an object-location memory scene recognition task in which, on some trials, the viewpoint between presentation and test was changed, either over a small angle or over a large angle to dissociate the use of different frames of reference. Besides children’s ability to make a correct ‘coarse’ judgment of an object’s location in the scene under different viewpoint conditions, we were interested in children’s ability to reproduce categorical and coordinate spatial relations after a viewpoint change. Although participants performed worst on the large viewpoint-change condition, which measured participant’ use of an allocentric reference frame, in all task conditions mean performance was above chance level. This suggested that the first five years reflect an important time-period for maturational changes in the neural systems related to reference frame use, and the age differences in overall performance might show that small maturational changes take place afterwards. In addition, participants performed better on the categorical trials compared to the coordinate trials, showing that children use these relations to memorize object locations.

3.1 Introduction

For orientation and navigation purposes it is important for adults as well as children to be able to locate objects in their environment. The most elementary mean of memorizing the location of an object in space is by a visual 'snapshot' in which an array of objects is stored as an 'integrated' picture (Simons & Wang, 1998; Wang & Simons; Burgess et al., 2004). This way of representing space is only useful when one does not change their viewpoint after studying a specific scene, for example when re-entering a room from the same entrance. Alternatively, one can code the spatial relation between one's own body and the target object, i.e. an egocentric reference frame, or the relation the target object has with other objects in the environment, i.e. an allocentric reference frame. The use of an egocentric reference frame seems to be specifically relevant for goal-directed motor actions, whereas an allocentric reference frame would be more useful for wayfinding behavior in complex environments, when movement over time plays a significant role. If one's viewpoint is changing over time, it would make sense to represent the location of object's with respect to the external environment rather than with respect to oneself (Burgess, 2008; Byrne & Becker, 2008; Hartley et al., 2003; Klatzky, 1998; Mou et al., 2004; Nadel & Hardt, 2004). It has been shown that, in the encoding of spatial layouts, both egocentric and allocentric reference frames operate in parallel (Mou et al., 2004: Nadel & Hardt, 2004), possibly even already at the age of three years (Nardini et al., 2006).

Functional neural imaging data (Hartley et al., 2003; Iaria et al., 2003) and neuropsychological studies (King et al., 2002; King et al., 2004; Spiers et al., 2001) support the dissociation of different reference frames in adults. It has been shown that the egocentric reference frame depends on the striatum, while the use of an allocentric reference frame requires the hippocampus (Iaria et al., 2003; Maguire et al., 1998). For instance, compared to normal healthy subjects, it was shown that hippocampal patients' performance on spatial memory tasks is impaired (Bird & Burgess, 2008), in particular on scene recognition tasks (Carlesimo et al., 2001; Holdstock et al., 2005; Taylor et al., 2007). A good example of hippocampal involvement in the representation of an object's location in an allocentric frame of reference is given by King and colleagues (2002). They showed that a patient with focal hippocampal pathology performed significantly worse on an object-location memory scene recognition task in which the viewpoint was changed between presentation and test, while his performance was similar to that of controls when the viewpoint on the scene remained stationary. For this latter task either an egocentric or an allocentric reference frame would have sufficed to solve the task. Yet, the viewpoint-change task required allocentric processing, which either meant representing an object's location with respect to other objects in the scene, or by mentally manipulating one's viewpoint from the stored (egocentric) representation to the viewpoint at test, e.g. a three-dimensional framework is provided in which movements of viewpoint can be calculated (King et al., 2004).

An interesting question arises as to how the processing of different reference frames and related neural structures changes with age. Therefore, in the present study, we investigated whether and to what extent children of different age groups can apply different reference frames. In turn, this may inform us about the functional maturation of neural structures related to the use of different reference frames. Children 5 to 10 years were tested on an object-location memory scene recognition task similar to the task of King and colleagues (2002) as described above, in which, between presentation and test, the viewpoint on the scene was either identical or shifted. In addition to the original paradigm, we differentiated between small and large viewpoint changes, so that the use of a visual snapshot and the use of an egocentric frame of reference could be dissociated. In case of a viewpoint change, participants would not succeed if they had used a visual snapshot strategy to encode the scene. Since in the small viewpoint change the objects' locations in the scene with respect to the participant's body and the locations of the objects within the scene were kept constant, the use of an egocentric or allocentric reference frame would lead to success. However, in the large viewpoint-change condition, the only way to solve the task was through allocentric processing, by representing an object's location in relation to the external environment of the scene, or by mentally manipulating one's viewpoint from the stored (egocentric) representation to the viewpoint at test.

Orthogonal to the choice of reference frame, one can store object locations according to different grains of spatial relations. That is, spatial relations between one's own body and an object (egocentric) or between objects in the environment (allocentric) are thought to be processed at mainly two levels of detail; a fine-grained level, i.e. distance and direction, and at a categorical level, representing a general spatial category (Huttenlocher et al., 1991). In object location memory, these two levels combine: when uncertainty about an object's coordinates increases we rely more on categorical relations. For example when the amount of time over which an object's location has to be remembered is greater (Huttenlocher et al., 1991; Postma et al., 2006); it is easier to remember that the keys were on the table rather than to remember their exact position in space, i.e. a certain distance from the edge of the table. Similarly, uncertainty about an object's location can also vary with the angle over which one's viewpoint changes, or the amount of viewpoint changes over time, i.e. during wayfinding in a complex environment. In this case, again, with the use of abstract, invariant category information, it is more easy to relocate objects than with exact metric information; it is more difficult to recalculate the exact distances between oneself and an object (or between objects) when observing a scene from a different perspective than to remember a prototypical spatial category to which an object belongs. In the scene recognition task used in the present study, the processing of categorical and coordinate spatial relations were dissociated by asking for a fine judgment in which the distractor items varied categorically or coordinately after participants had made a coarse judgment of an object's location (measuring participants' reference frame use). Given the fact that categorical judgments allow a degree of constancy over viewpoint changes (Postma et al., 2006), we might expect a stable performance on the categorical judgments, thus one that is not affected by viewpoint changes. On the other hand, performance on the coordinate spatial relations might possibly vary with the angle over which one's viewpoint changes. In addition, the constancy of categorical judgments and the variation of coordinate judgments with viewpoint change may vary for the children in different age groups.

3.2 Method

3.2.1. Participants

Fifty-nine children from two primary schools in the Netherlands participated in the study. The children were divided in three different age groups: 5-year-olds (n = 20, mean age = 5.9, *SD* = 0.47, number of girls = 10), 7-year-olds (n = 20, mean age = 7.96, *SD* = 0.42, number of girls = 10) and 10-year-olds (n = 19, mean age = 10.14, *SD* = 0.49, number of girls = 9). Informed consent was obtained from the parents of the children. All children reported to be healthy, had normal or corrected to normal vision and were unaware of the rationale of the study.

3.2.2. Apparatus and Stimuli

The scene recognition task, is a computer task with which participant's object location memory can be assessed. The task consists of color pictures based on accurate three dimensional projections of realistic spaces in which several common objects were located. In the encoding phase of the task, on each trial, one of the rooms was shown for 15 seconds and participants were asked to carefully look at the picture of the room, since subsequently, he/she would be asked to relocate six objects (one-by-one in random order) that were present in the room. In the test phase, an object was shown for 2 seconds on a white background. Next, the picture of the room was presented again, however, now without the six to-be-relocated objects. The participant was asked to choose the coarse correct location from three possible locations indicated by colored outlined squares. We controlled for the likelihood of the three different locations: from the three locations the location that appeared not the most likely and not the least likely location, was chosen as the target location. The other two positions were distractors. The colors of the squares corresponded to differently colored stickers on three keys (F, G, and H) of the computer keyboard. In case of a correct choice, three colored dots at the location of the correct square (again corresponding to the three keys), replaced the squares. By choosing one of the dots, participants were asked to give a more fine-grained estimation of the location of the object in the room. The distractors of this fine-grained judgment differed from the correct location in a categorical or coordinate way, for example, in case an object was located at the table, the distractors were placed next to the table or underneath the table (categorical distractors) or in a different location at the table (coordinate distractors). In case the participant had chosen the incorrect square, he/she directly proceeded to the next trial. There were no time restrictions on participants' choices, nor was a fast response encouraged. During the test phase of the study the picture of the room could include a small (thirty degrees) or a large (ninety degrees) viewpoint change, which only included a rotation (and not a translation). As explained in the introduction, in case of a large viewpoint change, participants could not solve the task if they had remembered the locations of the objects either by using a visual snapshot or by remembering the location of the objects with respect to their own body. The only way to correctly solve this task was through allocentric processing, by representing an object's location in relation to the external environment, or by mentally manipulating one's viewpoint from the stored (egocentric) representation to the viewpoint at test. One third of the pictures was identical to the encoding phase pictures, one third included a small viewpoint change, and one third a large viewpoint change. Viewpoint changes were as often to the left as to the right. Thus, for each room four objects had to be relocated of which the viewpoint was different between presentation and test. Two versions of the task were used to match the categorical and coordinate response options across the objects, i.e. in one version participants were required to make a coordinate judgment about an object, whereas, in the other version participants had to make a categorical judgment about the same object.

3.2.3. Procedure

The scene recognition task (for an example see Figure 3) was presented on a 15-inch computer screen, and participants were seated approximately 60cm from the screen. Before the test trials, the experimenter read out loud the instructions from the computer screen. When the instructions were fully understood, the children were familiarized with the stimuli through a practice trial in which they were shown a room, and were asked to relocate three objects as described in the previous section. The room shown on this practice trial was similar for all subjects. After the practice trial, participants were once more asked whether they had understood the task and they had indication that this was the case, official testing started. The task consisted of 15 rooms with six objects each, leading to 90 test trials in total. The rooms and the objects within the rooms were presented in random order.

3.3 Results

For both for the coarse judgments which measured participant's use of a particular reference frame, and the fine judgments which measured participant's ability to code categorical and coordinate spatial relations in a scene, a repeated measures analysis of variance (GLM) was conducted for the proportion of correct answers, with Age Group (3) as between-subjects factors and Viewpoint Change (3) as within-subjects factor. In the repeated measures ANOVA for the fine judgments, the extra within-subjects factor Type of Spatial Relation (2) was included. In both analyses a significant main effect was found for the factor Age Group, coarse: F (2, 56) = 28.25, $p < .001$; fine: F (2, 56) = 17.84, $p < .001$. Bonferroni corrected post hoc analyses showed that all age groups performed significantly differently from each other (p's > .05), with a better performance with age, see also Figure 1 and 2. Note that chance level was 33%, thus, overall, all age groups performed above chance level.

Furthermore, the analyses revealed a significant main effect for the factor Viewpoint Change, coarse: F (2, 112) = 9.81, $p < .001$; fine: F (2, 112) = 6.00, $p < .01$. Bonferroni corrected post hoc comparisons showed that, for the coarse judgments, participants' performance on the large viewpoint change condition (mean = 50%) differed significantly from participants' performance on the no viewpoint change (mean = 58%) and the small viewpoint change condition (mean = 54%). For the fine judgments, participants performance was significantly better in the small viewpoint change condition (mean = 62%), and not the no viewpoint change condition (mean = 58%), compared to the large viewpoint change condition (mean = 54%). The extra within-subjects factor in the analysis on the fine judgment also showed a significant effect, with all age groups performing better on the categorical trials (mean = 62%) than on the coordinate trials (mean = 54%). Thus, participants performed better when they were required to make a categorical judgment compared to a coordinate judgment.

For both the coarse and fine analyses no significant interaction effects were found between the factors Age Group and Viewpoint Change, coarse: F (4, 112) = 1.17, p > .05; fine: F (4, 112) = 1.63, p > .05., and none of the other interactions in the fine judgment analysis was significant; Age Group and Type of Spatial Relation, F (2, 56) = 0.83, p > .05; Viewpoint Change and Type of Spatial Relation, F (2, 112) = 0.99, p > .05; Age Group, Viewpoint Change and Type of Spatial Relation, F (4, 112) = 1.00, p > .05. Hence, beside the main effects, no interaction effects were obtained for these analyses.

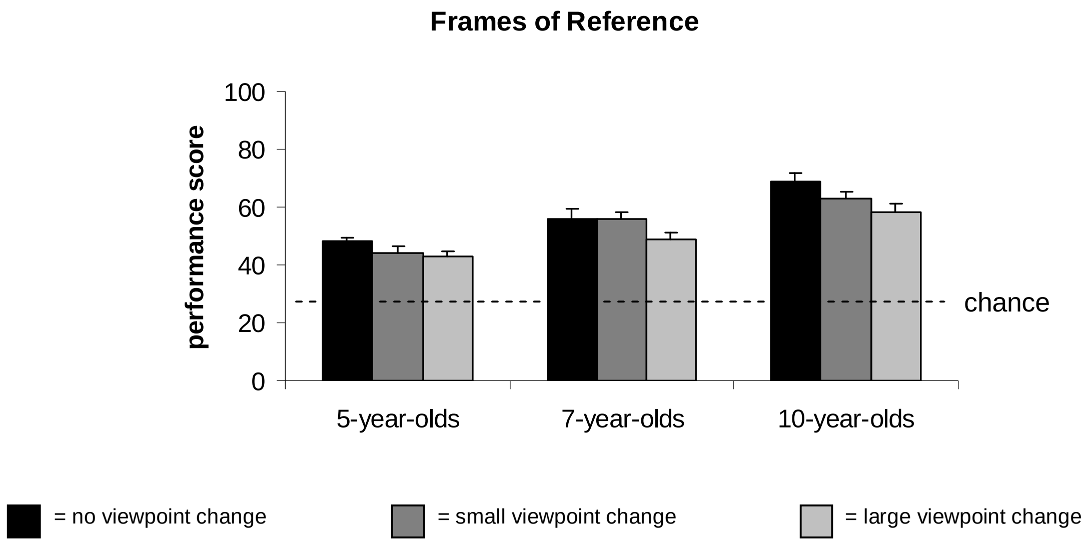


Figure 1. Participants' mean performance score (and SE) on the coarse judgements of the scene recognition task.

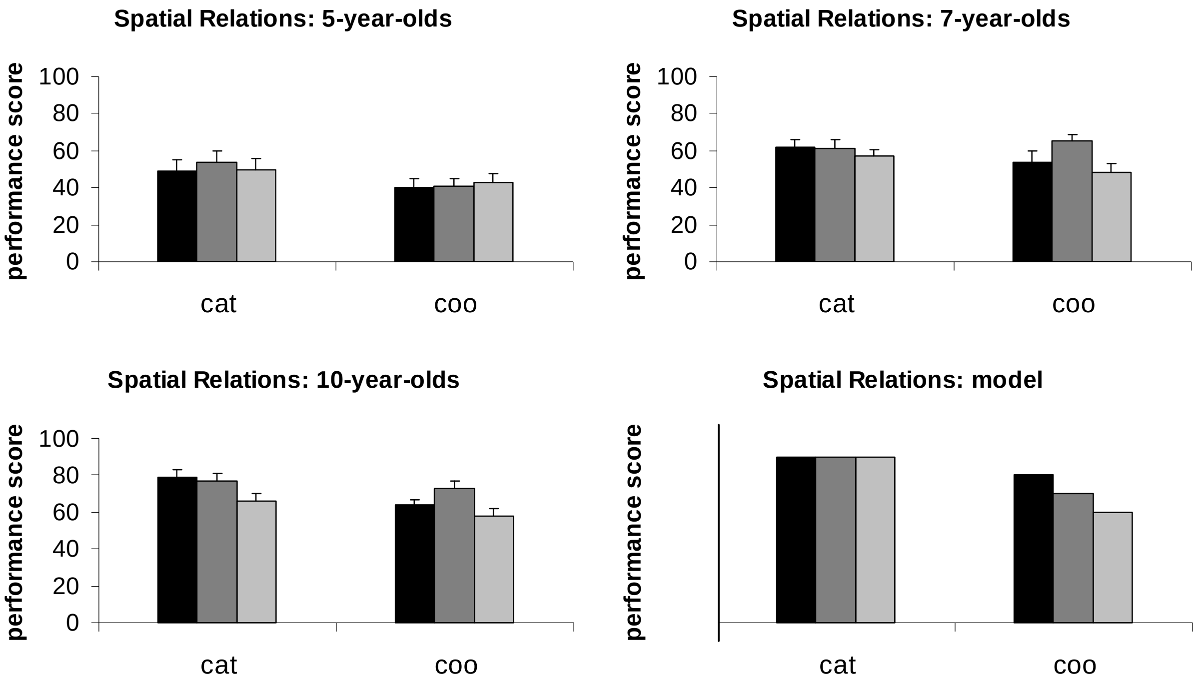


Figure 2. Participants' mean performance (and SE) on the fine judgments of the scene recognition task. In the bottom right we plotted what we expected, given the fact that categorical judgments, and not coordinate judgments allow a degree of constancy to viewpoint changes.

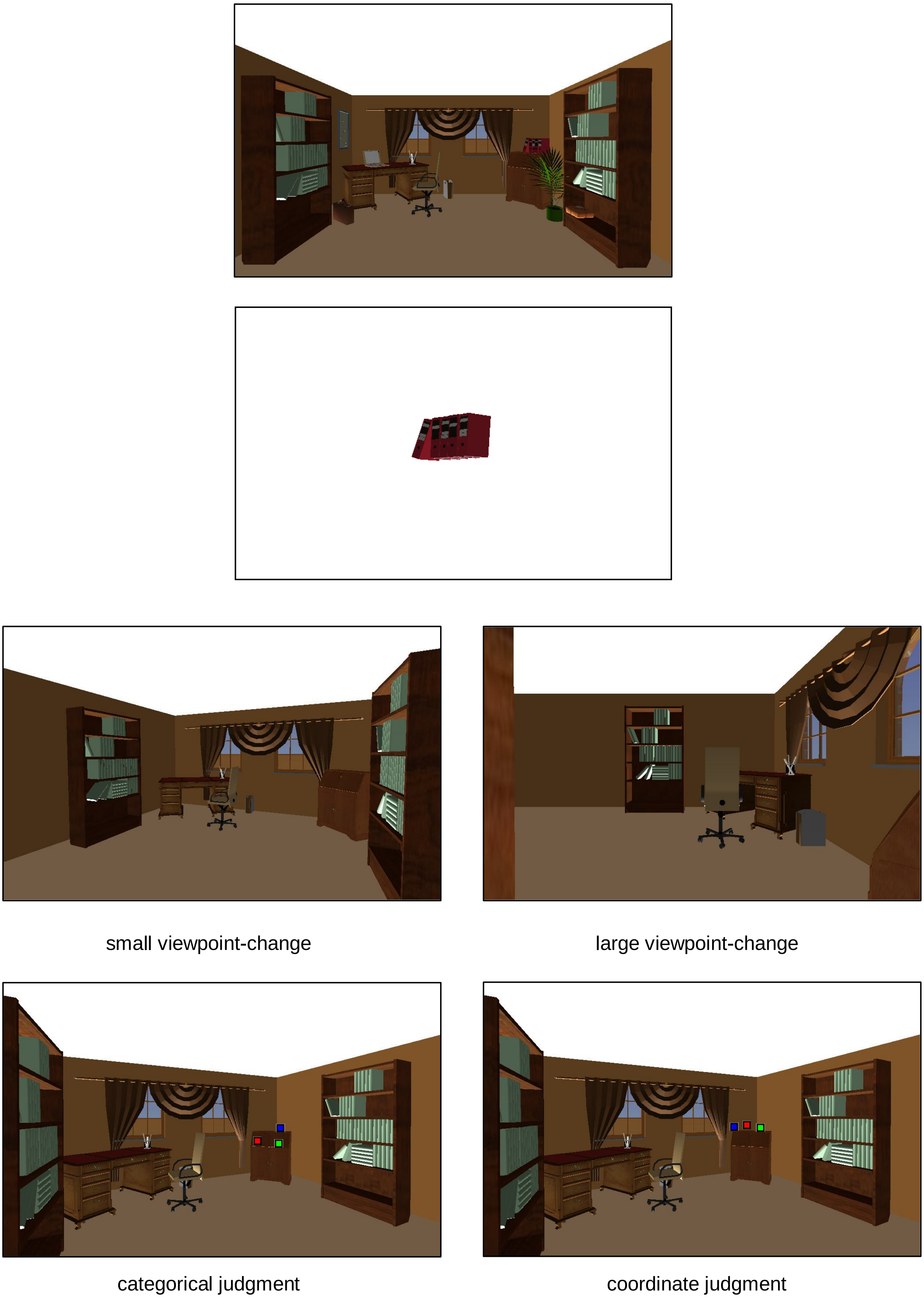


Figure 3. Example of a room picture used in the object-location memory scene recognition task, in the no viewpoint-change condition (on top), in the small viewpoint-change condition and in the large viewpoint-change condition.

3.4 Discussion

In the present study children 5 to 10 years of age performed an object-location memory scene recognition task in which, between presentation and test, the viewpoint on the scene was either identical or shifted. This manipulation made it possible to dissociate the use of different reference frames (King et al., 2002; King et al., 2004). In the no viewpoint-change condition, participants could use a visual snapshot and/or an egocentric frame of reference and/or an allocentric frame of reference to relocate different objects within the scene. In the small-viewpoint change condition, participants would succeed by using an egocentric and/or an allocentric reference frame. Finally, in the large-viewpoint change condition, only the use of an allocentric reference frame sufficed. In addition to children's ability to use different frames of reference, measured by a coarse judgment, we were interested in children's' ability to process categorical and coordinate spatial relations, measured by more fine-grained judgments.

For both the coarse and the fine judgments, significant main effects were found for age group and viewpoint change. First, the main effect for group showed that, although all participants performed above chance level on the task, the 5-year-old, 7-year-old, and 10-year-old children differed from each other in overall performance on the scene recognition task, with an increased performance with age. Second, overall all participants performed worst in the large viewpoint-change condition, when only an allocentric frame of reference sufficed to solve the task. In the coarse judgments, performance on this condition differed significantly from participants' performance on the no viewpoint-change condition and the small viewpoint-change condition. In the fine judgments, however, this large angle performance only differed significantly from participants' performance on the small viewpoint-change condition. Interestingly, for both coarse and fine judgments, no significant interaction was found between the factors group and viewpoint change. This indicates that the typical use of different frames of reference is already present at age 5 years, but that it becomes more effective with age.

The fact that for both coarse and fine judgments, participants' performance was significantly better in the small than in the large viewpoint-change condition could indicate two things; in the small viewpoint-change condition participants had used an egocentric reference frame and this was easier, or the use of egocentric and allocentric reference frames had an additive effect, which suggested that, during encoding, children had processed both frames of reference in parallel and with the availability of both reference frames performance increased. Evidence for the latter suggestion can be found in participants 'above chance' performance on the allocentric-only processing condition (large viewpoint-change condition). Participants did not know beforehand which viewpoint condition they would receive at test, thus it seems reasonable to suggest that they would not have performed above chance level on this condition if they had not encoded both reference frames in parallel. This suggestion extends the results of a study by Nardini and colleagues (2006), who showed parallel processing of egocentric and non-egocentric (i.e. either an allocentric reference frame and/or spatial updating by movement) reference frames in 3 to 6-year-old children. In addition, above chance level performance on the large viewpoint-change condition is in accordance with previous developmental studies showing that recognizable place learning, which implies the use of an allocentric frame of reference, can already be observed in 21-month-old children (Newcombe et al., 1998) and develops until at least 5 years of age (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003; Newcombe & Huttenlocher, 2000).

It should be acknowledged that young children's performance in the large viewpoint change condition is a conservative measure of the emerging ability to use allocentric processing (Nardini et al., 2006). An additional difficulty in the large viewpoint-change condition is to inhibit one's response provided by the egocentric frame of reference. In the present study we did not match the response options to this frame of reference, therefore, it could not be investigated whether the errors children made in the large viewpoint-change condition were indeed egocentric errors. For future studies, it would be an interesting extension to the task to place the distractors in locations that would be predicted by the use of an egocentric reference frame, so that this possibility can be ruled out.

The alignment of the view at test with the view at presentation did not have an additional effect on children's recall accuracy, that is, the use of a visual snapshot of the scene did not significantly increase participants performance. Again, this finding could imply two things. First, the advantageous use of a visual snapshot in scene recognition (Simons & Wang, 1998; Wang & Simons, 1999, but see also Burgess et al., 2004) only develops after the age of 10 years. This does not seem very plausible, however, since a visual snapshot is considered the most elementary mean of representing the location of an object. Second, it might be possible that, if the viewpoint on the scene only changes to a small extent (as is the case in the small viewpoint-change condition), children can still use a visual snapshot strategy to solve the task. Future studies could test the tenability of these possibilities.

In addition to children's ability to use different frames of reference, we investigated their ability to process specific spatial relations (Bullens & Postma, 2008; Huttenlocher et al., 1991). Previous research showed that we rely on categorical relations when uncertainty about an object's coordinates increases (Huttenlocher et al., 1991; Postma et al., 2006), for example when one's viewpoint changes. For this reason, we expected to find a stable response pattern for the categorical judgments, thus in which the viewpoint changes would not affect participants' performance. For all age groups, we indeed found a stable performance for the categorical judgment across the three different viewpoint-change conditions. However, this was also the case for the coordinate judgments, for which we would have expected a worse performance with greater changes in viewpoint. Therefore, the current child data do not support the 'uncertainty with viewpoint change' model which we proposed. Importantly, a main advantage was found for the categorical trials on the scene recognition task, suggesting that already at the age of 5 years, children rely on these relations to locate objects. Huttenlocher and colleagues (1994) observed that children as young as 16 months of age were able to correctly locate objects in a sandbox, proving young children's ability to combine fine-grained information with categorical information. However, a different pattern of bias existed compared to 10-year-olds and adults, indicating that, when uncertain, young children use different category information than older children and adults. Thus, the reason that we did not obtain the expected viewpoint change effect for coordinate spatial relations, might be due to the fact that children younger than 10 years weight categorical and coordinate information differently than older children and adults (Newcombe & Huttenlocher, 2000). This might be related to their limited processing capacities (Sandberg, 1999).

The present results give some suggestions regarding the functional maturation of the underlying neural structures. Studies using functional neural imaging techniques have shown that, for adult humans, the egocentric reference frame is supported by the striatum, while the use of an allocentric reference frame is supported by the hippocampus (Hartley et al., 2003; Iaria et al., 2003). The results of the present study might support the notion that the first five years reflect an important time-period for maturational changes in these neural systems (Newcombe & Huttenlocher, 2000; Overman et al., 1996), and that only small maturational changes take place afterwards. Possibly, these maturational changes will be stimulated by experience (Greenough et al., 1987 and Shonkoff & Philips, 2000 in Newcombe et al., 2007), suggesting a (bi-directional) interaction between biological maturation and experience (Newcombe et al., 1998).

CHAPTER 4

THE ROLE OF LOCAL AND DISTAL LANDMARKS IN THE DEVELOPMENT OF OBJECT LOCATION MEMORY

Bullens, J. & Postma, A. The role of local and distal landmarks in the development of object location memory. (*submitted for publication*)

Abstract

In order to locate objects in an enclosed environment animals and humans use visual and non-visual distance and direction cues. In the present study, we were interested in children's ability to relocate an object on the basis of self-motion cues and local and distal color cues for orientation. Five to 9-year-old children were tested on an object location memory task in which, between presentation and test, the availability of local cues and distal cues were manipulated. Additionally, participants' viewpoint could be changed. Interestingly, children's overall performance (i.e. absolute distance score) showed that they relied on self-motion cues in case landmarks were not present. Moreover, angular errors indicated that children relied on the orientation provided by distal landmarks when changing viewpoint. These results are discussed in terms of the adaptive combination model, proposed by Newcombe and Huttenlocher (2006), which states that different information sources are weighted differently over the course of development.

4.1 Introduction

Object location memory is important for orientation and navigation. Two types of sensory inputs appear crucial: visual and proprioceptive (i.e. body movement) information. They help to mark an object's location in relation to one's own body (egocentric reference frame) or in relation to one's own movement (egocentric spatial updating), in relation to a configuration of local and/or distal landmarks (allocentric reference frame) and/or in relation to the geometry of an enclosed environment (Hermer & Spelke, 1994; 1996; Klatzky, 1998; Mou et al., 2004; Nadel & Hardt, 2004). Although the latter has also been proven to be of importance in understanding the development of spatial cognition (Cheng & Newcombe, 2005; Learmonth et al., 2008; Nardini et al., 2008), in this study we specifically focused on children's ability to use self-motion cues in combination with local and distal landmarks to orient in space. That is, the geometry of an environment (i.e. a square room) may provide a strong basis for coding where things are located within that environment (Hermer & Spelke, 1994; 1996), only when one keeps track of orientation (i.e. "which wall is north"). Visual local and distal landmarks can serve as orientation cues (Hamilton et al, 2007; 2008) and they can provide a basis for coding location, called place learning (Morris, 1981; Tolman et al, 1946). In the present study, we were specifically interested in landmarks as orientation cues.

Newcombe and colleagues (1998) studied the ability of 16 to 36-month-old children to combine the use of visual and movement information when walking to a different position in a testing room before relocating an object in a rectangular sandbox. It was demonstrated that all children were able to correctly search for hidden toys after, between presentation and test, having walked to the opposite side of the sandbox. Even when at presentation (and test) the distal landmarks were not available, all children performed above chance level on the task, suggesting that reliable movement information (egocentric spatial updating) is already present early in life. Moreover, it was shown that only for the children older than 21 months performance improved with the availability of the visual distal landmarks at presentation. Thus, unlike the movement information, visual cues present in the testing room can only be used from a certain age. The present study extended this previous work in two ways: first, by allowing a full combination of local landmark and distal landmark availability, and second, by changing the function of these landmarks from providing a basis for the direct coding of location (as in the study of Newcombe et al, 1998) to providing a basis for orientation (Hermer & Spelke, 1994; 1996).

The notion that distal visual landmarks can provide a basis for orientation has been indicated by various object location memory studies focusing on enclosed spaces (Hamilton et al, 2007; 2008; Hartley et al., 2004). In these studies, respectively rats and humans used the absolute and relative distances from the wall(s) of the enclosed environment in combination with distal landmarks for orientation in order to correctly relocate an object. The abstract representation of a location in terms of 'distance(s) to (a) wall(s)' is consistent with the neural representation of a location formed by the firing of place cells in the hippocampus of animals and humans (Ekstrom et al., 2003; Morris et al., 1982; O'Keefe, 1976; Ono et al., 1991; Packard & McGaugh, 1996; Pearce et al., 1998). Importantly, orientation provided by the distal landmarks is most likely maintained by the head-direction cells (Taube, 1998). Clearly, head direction cells seem to form a fundamental neural basis for location memory in animals as well as in humans. At present, more insight in their neurocognitive maturation is needed. In the current study, we were interested in children's use of local and distal landmarks for orientation. Extensive literature exists on children's ability to reorient in an enclosed environment using 'distal' landmarks (for a review, see Cheng & Newcombe, 2005). Although, it is known that, when local and distal landmarks conflict, 5-year-old children orient towards local cues, whereas children orient towards distal cues from 7 years onwards (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003), no systematic investigation has been done into children's use of different landmark types for orientation in non-conflicting situations (Newcombe et al., 1998).

Studies examining children's ability to orient in an enclosed environment using distal landmarks, all used the typical orientation paradigm. In this paradigm a desirable object is hidden in the corner of a rectangular room, of which one of its walls is painted in a distinctive color. Only the combined use of the surface geometry of the testing room and the landmark information represents the correct location of the object. It was shown that when 20-month-old children were tested in a small testing room (4 by 6 feet) they ignored the distinctive colored wall, performing at chance level (Hermer & Spelke, 1994; 1996), and only 5 and 6-year-old children were able to solve the task (Hermer-Vazquez et al., 2001). However, in case children were tested in a large testing room (8 by 12 feet), they combined geometric information with landmark information (Learmonth et al., 2002; Learmonth et al., 2001) at already 18 months. Recently, it has been opted that the traditional reorientation paradigms contained a bias towards the use of the geometry of the room. Without this bias, even in a (relatively) small square room, children 18 to 24-month-old employed colored landmarks for orientation (Nardini et al., 2008). The children's initial preference for geometry over the use of landmarks in small enclosed spaces, can be explained by the adaptive combination model, which proposes that different sources of information (geometry and landmarks) are weighted differently in different situations, depending on factors such as the certainty with which the information sources are encoded, their salience and their perceived usefulness (Learmonth et al., 2008; Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007). In the present study, we were interested in whether children 5 to 9 years of age could combine the use of self-movement information in combination with visual information for orientation in order to correctly relocate an object. In addition, we were interested in children's dependency on local and/or distal landmarks for orientation. Children 5, 7 and 9 years of age were tested on an object location memory task in which, between presentation and test, the availability of local cues and distal cues were manipulated and/or participants' viewpoint was changed.

4.2 Method

4.2.2. Participants

Forty-six children 4-9 years from the Violenschool in Hilversum, the Netherlands, participated in the study. The children were divided in three age groups: fourteen 5-year-olds (mean age = 5.0, *SD* = 0.09 years, 7 girls), sixteen 7-year-olds (mean age = 6.9, *SD* = 0.08 years, 8 girls) and fifteen 9-year-olds (mean age = 9.0, *SD* = 0.06 years, 7 girls). One 5-year-old was excluded from the analyses, since this child adopted a strictly egocentric response strategy, thus relocating the target object with reference to his own body, and therefore the potential influence of availability of distal cues, room cues and/or body movement cues could not be assessed. All parents gave their consent for their child's participation. The study was approved by the ethic committee of Utrecht University.

4.2.3. Apparatus and Stimuli

The square room in which the children were tested was formed by 11 poster boards (width 90cm, and length 200cm), which were all covered with black curtains, see Figure 1 for the set-up. Above the poster boards, only white painted walls and a white painted ceiling with a light, located directly above the centre of the square room, were visible. The entrance to the room was created by an opening between two poster boards, which was also covered with black curtain after having entered the room. The test apparatus, i.e. a square table (60cm x 60cm) with, on top, a sheet of glass (52cm x 52cm), was placed in the middle of the room. A square wooden frame (60cm x 60cm x 4cm to the inside) with on one (e.g. bottom) side four coloured sides (red, blue, yellow and black), and on the other (e.g. on top) side four black sides, was placed on top of the table, and either or not served the purpose of a local cue. Four coloured (orange, purple, green and beige) A1 sized pieces of paper which were attached (at eye-level for the children) to the black curtains on each side of the room, acted as distal cues. The distal cues were covered with black cloth in case the children were tested in the no distal cues condition. Two laminated pieces of paper (both 52cm x 52 cm) were placed on top of a wooden table-leaf, located 5cm under the top of the table, and underneath the sheet of glass. One of the laminated pieces of paper was secured to the wooden table-leaf and depicted a grid with coordinates. Also, on this paper the 25 possible target locations, which were arranged in a grid (5 x 5), were marked. During testing, an all white laminated piece of paper covered the view of the coordinates and the target locations. On the floor and surrounding the table, a square (136cm x 136cm) was marked with white tape. This was done in order to guide the children to walk in a straight line and to turn 90 degrees at the corners. The target consisted of a pawn, as used in board games. At the start, children could choose which pawn they wanted to play 'the game' with.

4.2.4. Design and Procedure

The task was to memorize the exact location of the pawn on the square table. Participant's viewpoint and the availability of local and/or distal cues varied along a 2x2x2 design in which participant's viewpoint either or not changed and in which either both type of cues, only local cues, only distal cues, or no cues were available, see Figure 2. On each trial the children walked a fixed distance between encoding and retrieval, independent of the viewpoint factor. That is, they either walked to their new viewing position or they walked halfway and back to their original viewing position. The walking direction varied randomly. All participants completed one practice trial and two blocks of eight test trials, in which one of each of the eight conditions was included. Within the blocks, the trials were presented randomly. Of the 25 possible predetermined target locations, which unbeknownst to the participants were arranged in a grid, the location at the centre (of the square table) was always used for the practice trial. This was done to familiarize the children with the procedure, without demanding too much cognitively. On each test trial the target was placed randomly on one of the 24 remaining hiding locations, of which 16 in total were used for each child.

During testing, one experimenter placed the pawn in the correct location, if necessary removed cues between the encoding and retrieval phase, and recorded the responses of the child. The other experimenter walked with the child to the right viewing position, and distracted the child while the first experimenter was recording the responses in order to make sure the children did not take notice of the sheet of paper with coordinates and possible target locations. Each trial, the child was first asked to take a good look (approximately 5 seconds) at the pawn and to remember its position. Thereafter, the child was assisted by the second experimenter in walking (face up and forward) to the correct viewing position thereby making sure that the child did not fix his/her gaze on the correct location. Meanwhile, the first experimenter removed the pawn from the table. After having reached the correct viewing location, the child was asked to close his/her eyes and together with the second experimenter count to ten out loud. During this time, the first experimenter could remove or cover local and/or distal cues. Subsequently, the child was provided with the pawn and asked to place it back in the correct location. Although children were encouraged several times during testing, no specific feedback was provided about the accuracy of responses. After the first experimenter had recorded the response, a new trial started. Before actual testing, the children completed a practice trial in which they changed viewpoint and in which both cues remained available. Also, in order to make sure that the first experimenter did not function as a cue, he/ she constantly moved around.

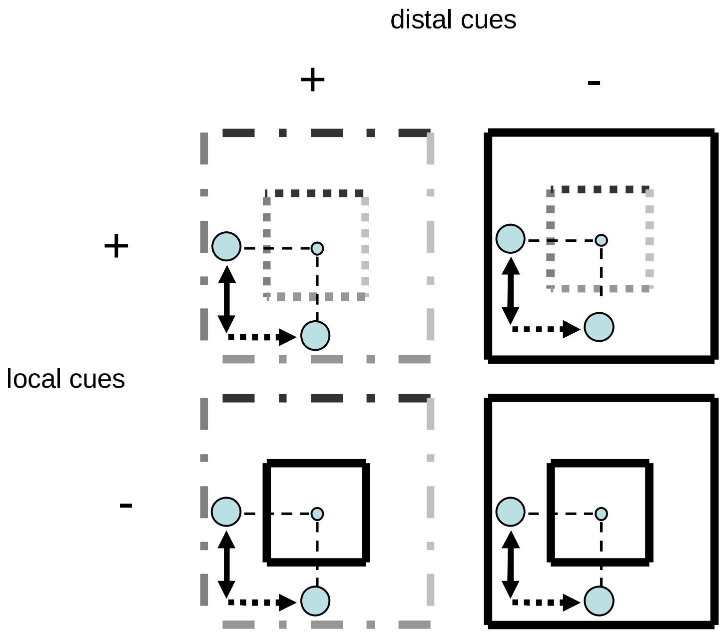


Figure 2. Experimental design of the study: participants were asked to relocate an object at the square table (the small square inside the larger square which depicted the square room in which testing took place), and between presentation and test the availability of local color cues (on the sides of the square table), and distal color cues (on the sides of the square room) was manipulated. Furthermore, participants were either or not required to change their view (depicted by the arrows) between presentation and test.

4.3 Results

4.3.1. Overall performance

Children's overall performance was calculated on basis of the distance error between a subject's response and the target object's true location. Since raw distance (cm) does not provide an equivalent measure of performance for objects near the edge and those near the centre of the square table (i.e. with the latter having smaller distance errors by chance), the distance errors were transformed to a standardized performance score, with the following formula: 100 x (chance distance – error distance) / chance distance (see Nardini et al., 2006). This standardized score is equivalent across locations because it is scaled against the level of performance that would be expected by chance, which was calculated as the average of the distances from each possible response locations to the correct location. Following this transformation, a score of 0 indicates chance performance, while a score of 100 indicates a correct search. A score below 0 indicates an error greater than that expected by chance. It was shown that the children performed well above chance level in all four conditions.

The standardized performance scores were subjected to a repeated measure ANOVA with View (2), Distal Cues (2) and Local Cues(2) as the within-subjects factors and Group (3) as the between-subjects factor. The analysis revealed a significant main effect of Group (F (2,42) = 8.75, p = .001). Importantly, all age groups performed significantly above chance level, 5-year-olds, t (13) = 9.11, p < .001; 7-year-olds, t (15) = 22.97, p < .001 and 9-year-olds, t (14) = 36.89, p < .001. In addition, post hoc comparisons (Bonferonni corrected) showed that overall performance of the youngest children (5-year-olds, mean = 54.1) differed markedly from the oldest children (9-year-olds, mean = 77.3) tested, while the 7-year-olds (mean = 66.2) did not statistically differ from either of both age groups. Also, a main effect for the factor View was found, F (1,42) = 14.48, p < .001, showing that, overall, children performed significantly better in the no viewpoint change condition (mean = 71.3) compared to when their viewpoint changed between presentation and test (mean = 60.4). No further main or interaction effects were obtained for this analysis, i.e. no interaction was found between the factors View and Local Cues (F (1,42) = 0.19, p > .05) or View and Distal Cues (F (1,42) = 0.19, p > .05). To gain further insight in if the children in the different age groups had used the local and/or distal cues, for orientation in specific, the angular errors were measured.

4.3.2. Angular errors

The angular error (in degrees) was the angle between the original target location and the response location to the centre of the square table. Angular errors made by chance were 90 degrees, thus, similar to the overall performance score, standardized scores were calculated with the formula: 100 (90 – angular error) / 90. Again, a score of 0 indicated chance performance, a score of 100 indicated a correct search, and a score below 0 indicated an error greater than expected by chance.

The standardized scores for angular errors were also subjected to a repeated measure ANOVA with View (2), Distal Cues (2) and Local Cues(2) as the within-subjects factors and Group (3) as the between-subjects factor. First of all, no significant effect was found for the between-subjects factor Group (F (2,42) = 2.62, p = .085). That is, although performance increased with age, the differences between the age groups was not statistically significant. Furthermore, in the analysis no interaction effects were found between the factor Group and the within-subjects factors View (F (2,42) = 0.21, p > .05), Local Cues (F (2,42) = 1.35, p > .05), and Distal Cues (F (2,42) = 1.72, p > .05), showing that there was no change in relative use of self-motion, local or distal cues in the age range studied, i.e. the children get (non-significantly) better overall, but do not specifically improve on one cue type more than others. However, there was a significant main effect for the factor Local Cues (F (1,42) = 5.25, p < .05), which indicated that, overall, children performed better on the angular measure when the local cues were available during retrieval. Most interestingly, though no main effect was found for the factor Distal Cues (F (1,42) = 0.25, p > .05), the interaction between the factors View and Distal Cues reached significance, F (1,42) = 5.58, p < .05; a post hoc analysis (Bonferonni corrected) showed that the children performed significantly better in the viewpoint-change condition when the distal cues were available (t (45) = 2.01, p = .05), while this was not the case for the same viewpoint condition (t (45) = -1.40, p > .05). Importantly, a One Sample T test with adjusted alpha showed that, in the viewpoint-change condition, children's performance did not significantly differ from chance (i.e. making angular errors that were clustered around 90 degrees) when the distal cues were not available; t (45) = 0.58, p > .05, while performance was above chance level when distal cues were available, t (45) = 3.81, p < .001. It thus seems that the distal cues were used specifically to help process a change of view, not otherwise. No further main or interaction effects were obtained.

4.4 Discussion

The objective of the present study was twofold. In the first place we were interested in whether children 5 to 9 years of age could combine the use of self-movement information in combination with visual information for orientation in order to correctly relocate an object. In addition, we were interested in children's dependency on local and/or distal landmarks for orientation. Children 5, 7 and 9 years of age were tested on a location memory task in which, between presentation and test, the availability of local cues and distal cues was manipulated, and children's viewpoint could change.

First of all, regarding the overall performance score, it is important to note that all age groups performed significantly above chance level, even in the condition in which no visual information was available at test. This means that all children were able to rely on their self-movement cues, which was particularly important when distal cues were not available. This finding is consistent with the results obtained by Newcombe and colleagues (1998). Furthermore, it was shown that overall performance of 5-year-olds differed markedly from the 9-year-olds, indicating that the older children were more precise in their estimations in terms of the combined use of distance and direction. In addition to a group effect, a main effect was found for the factor viewpoint, showing that all children performed better at the task, when the viewpoint was similar between presentation and test. This result also corroborates the findings of Newcombe and colleagues (1998). Notably, no overall performance effect was found for (distal) landmarks availability. That is, participants did not perform better when the landmarks were available, compared to when they were not, suggesting only self-movement cues at presentation were used for this behavioral aspect.

Importantly, angular errors, which provided a measure for the orientation of the response (in contrast to ‘overall performance’ in which the combination of direction and distance was central) did reveal outspoken landmark effects. To our knowledge, none of the object location memory studies conducted so far have made a clear distinction between the use of local and distal landmarks as orientation cues. Here we observed that all children performed better on the angular measure when the local cues were available at test, suggesting that all age groups had processed these cues at presentation and took advantage of them at test. This result is in accordance with previous studies showing that, in conflict situations, at already the age of 5 years children spontaneously use local cues for coding location (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003). Additionally, we showed that children use local landmarks for orientation in a non-conflicting situation. Thus, independent of change in viewpoint and/or the manipulation of the availability of distal landmarks, local cues helped children 5 to 9 years to orient in space.

No main effect for the factor distal cues was found, however, an interaction effect with viewpoint reached significance: all age groups performed significantly better on the angular measure in the viewpoint-change condition when the distal cues were available, while this was not the case for the same viewpoint condition. This finding suggested that the distal cues were used specifically to help process a change of view, and not otherwise. Furthermore, when participants did change viewpoint and the distal landmarks were not available, they performed at chance level. Thus, in order to perform at least above chance level when changing viewpoint, they needed the distal cues to remain oriented in the environment. Note, however, that participants performed well above chance level on the overall performance score in the ‘viewpoint change and no distal landmarks available’ condition. In all, it might be concluded that for general coding of location (including distance and direction) in a non-conflicting situation, participants rely on self-motion cues in case the distal landmarks fail to deliver, whereas, the orientation of the response (and thus participants’ orientation) seems to be well dependent on the availability of the distal landmarks when changing viewpoint in an environment.

Notably, angular errors did not reveal any group main or interaction effects. Although older children performed better on the angular measure than younger children, again with all three age groups scoring above chance level, this difference was not statistically significant. Since judging angle required the use of local cues, distal cues and/or self movement cues, this finding suggests that these cues are available to an equal level in the current age range. In addition, the fact that no interaction effects with the factor group were found indicates that, with age, children do not improve on one cue type more than the other.

In agreement with Cheng and colleagues (2007), young children can thus use self-movement cues as a reference system in a non-conflicting situation (Huttenlocher et al., 1998), and in a conflict situation (Nardini et al., 2008), but also as a back-up system if the preferred cue(s) (i.e. local and distal landmarks) fail(s) to deliver. According the adaptive combination model, the fact that, in the present study, children preferred the availability of local cues for orientation in general and the availability of distal cues for orientation during movement, might suggest that different landmark information and movement cues were weighted differently, depending on factors such as the certainty with which the information sources were encoded, their salience and perceived usefulness (Learmonth et al., 2008;

Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007). Future studies should more thoroughly test children’s ability to combine (integrate) information to locate objects in the natural environment. A good way to investigate the reliance on each source of information is to place the different information types in moderate conflict (i.e. not too large, since then integration behavior is unlikely) (Nardini et al., 2008). For example, to test children’s ability to integrate local and distal visual landmarks, between presentation and test, these cues should be moved with respect to each other (i.e. placed in conflict). Different theories (the ability to use a single landmark versus the integration of different landmarks) will lead to different expected outcomes (1. the child relocates the object with respect to the local landmark and does not use the distal landmarks; 2. the child relocates the object with respect to the distal landmarks and does not use the local landmark; 3. the child integrates both landmark types), and these expected outcomes might differ for children in different age groups, and can vary with, for example, the salience of the information sources. In addition, the geometry of the room (circular versus square) could be manipulated to test its effect on children’s ability to relocate objects. That is, a circular room only provides distance information and no shape information, and therefore should be a less accurate basis for coding location than a square room which does provide shape information. In turn, the use of colors as orientation cues can be contrasted in differently shaped environments.

CHAPTER 5

THE SPONTANEOUS USE OF NAVIGATION STRATEGIES IN CHILDREN 5, 7 AND 10 YEARS OF AGE

Bullens, J., Igloi, K., Berthoz, A., Postma, A & Rondi-Reig, L. The spontaneous use of navigation strategies in children 5, 7 and 10 years of age. (*in preparation*)

Abstract

Two essential navigation strategies can be separated; the sequential egocentric (i.e. route-based) strategy in which a sequence of body turns is remembered and the allocentric (i.e. map-based) strategy in which environmental landmarks are used for orientation. It has been suggested that both strategies are supported by the hippocampus, a brain region that is involved in the rapid encoding of information, and therefore should appear early in training. In the present study the parallel involvement of the sequential egocentric and allocentric navigation strategies in the learning process was examined in children 5, 7 and 10 years of age. With the use of a virtual reality task in which the different strategies could be dissociated it was shown that all age groups had encoded egocentric (body turn) and allocentric (landmark) information in parallel, already early in training. Though the 5-year-olds did show a preference for the egocentric strategy, they performed above chance level when required to use an allocentric strategy.

5.1 Introduction

In the literature on spatial cognition, two main navigation strategies, related to the usage of distinct reference frames, have been described: egocentric and allocentric strategies. Although the latter is well defined, as one that centers on aspects (i.e. geometry or landmarks) of the external environment and supports the creation of a flexible cognitive map (Burgess, 2006; O'Keefe & Nadel, 1978), the definition of the first seems to depend on the complexity of the wayfinding behavior that is described. In general, an egocentric strategy is defined as 'centered on the body', which means that a temporal sequence of body turns is learned. Recently, Rondi-Reig and colleagues (2006; see also Arleo & Rondi-Reig, 2007) introduced a further distinction between 'simple egocentric' (or also 'response') and 'sequential egocentric' (or also 'egocentric spatial updating') strategies. The simple egocentric strategy refers to associative S-R learning, as is the case in the T-maze paradigm in which rodents had to learn only one body turn (Packard & McGaugh, 1996) or as in the human radial arm maze in which participants could use a non-spatial counting strategy (i.e. from a single starting point counting the amount of arms [counter]clockwise) (Iaria et al., 2003). In the sequential egocentric strategy, on the other hand, multiple successive body turns are remembered. Hence, in contrast to a 'simple' S-R association, this strategy requires the temporal organization of multiple events.

Indirect evidence for the existence of different navigation strategies is their dissociation in terms of underlying neuroanatomical correlates; the (left) hippocampus supporting the sequential egocentric and allocentric strategy and the striatal system supporting the simple egocentric strategy (Burgess et al., 2002; Doeller et al., 2008; Ghaem et al., 1997; Iaria et al., 2003; Maguire et al., 1998; Packard & McGaugh, 1996; Rondi-Reig et al., 2006; White & McDonald, 2002). Since the striatum, through repetition of S-R associations, is specifically involved in the habituation of responses, it has been suggested that the use of an simple egocentric strategy typically appears at a 'late' stage in training (Iaria et al., 2003; Packard & McGaugh, 1996). The hippocampus, on the other hand, is involved in the rapid encoding of information (O'Keefe & Nadel, 1978), therefore both the allocentric strategy (Iaria et al., 2003; Poldrack et al., 2001) and the sequential egocentric strategy (Iglói et al., *submitted*) have been proposed to appear early in training. Several studies with humans (Iaria et al., 2003; Iglói et al., *submitted*; Maguire et al., 1998) and rodents (Packard & McGaugh, 1996; White & McDonald, 2002) have supported these different navigation-strategy related roles, defined by their appearance over time, for the hippocampus and the striatum.

Behavioral evidence for the use of allocentric as well as sequential egocentric strategies at an early stage in the learning process stems from a study by Igloi and colleagues (*submitted*). They tested adult humans on the StarMaze task, which is a virtual analogue of the StarMaze (Rondi-Reig, 2006) previously successfully used to asses navigation strategies in rodents. The task consists of a five arm radial maze in which participants have to navigate to a goal. During training, participants can use different strategies in order to (re)locate the goal. Intermitted probe trials allowed the assessment of the spontaneous strategies participants had used. The results showed that, across participants, both navigation strategies were used from the beginning of the task. Moreover, across probe trials, bi-direction switches in strategies were observed. Importantly, and similar to previous studies indicating that allocentric and simple egocentric strategies operate in parallel (Doeller et al., 2008; Nadel & Hardt, 2004), this study showed that, during training, participants had encoded the sequential egocentric and the allocentric strategy simultaneously. That is, the spontaneous use of a ‘corrected strategy’ in which, within one probe trial, participants first used a sequential egocentric strategy (e.g. sequence of body turns) and ‘corrected’ themselves using an allocentric strategy (e.g. environmental landmarks), implied the combined use of both strategies. This was further supported by the fact that, when forced to use either strategy, participants succeeded immediately in both.

An interesting question is whether the parallel involvement of the sequential egocentric and allocentric navigation strategies at a certain stage in the learning process develops with age. That is, the spontaneous use and/or the (in)ability to use these strategies at (a) specific moment(s) in time can give us more insight on the structural or functional development of brain areas related to navigation. A developmental study by Nardini and colleagues (2006) demonstrated that, in a ‘static’ spatial memory task, the adult ability to process egocentric and non-egocentric representations in parallel (Burgess, 2008; Nadel & Hardt, 2004) is already present in three-year-olds, and improves with age. Although developmental studies using virtual environments, in which amount and complexity of motion in time play a significant role, have investigated the effects of the regularity of the environmental structure (Jansen-Osmann et al., 2007), the presence or categorical function of landmarks (Jansen-Osmann & Fuchs, 2006; Jansen-Osmann & Wiedenbauer, 2004), and the types of exploration (Gabrielli et al., 2000) on children’s wayfinding behaviour, to our knowledge, no developmental studies have examined children’s navigation strategies in detail. More specifically, the time scale over which possible shifts between navigation strategies could take place has not yet been addressed.

Therefore, in the present study children 5, 7 and 10 years of age were tested on the virtual StarMaze task (Igloi and colleagues, *submitted*). The task consisted of two versions: a multiple strategies version and an allocentric version. In the multiple strategies version, it could be examined whether and, if so, in which phase(s) of the learning process participants had spontaneously used a specific navigation strategy. Also, potential switches between different strategies could be examined. The allocentric version of the task, on the other hand, investigated participants’ capability to use an allocentric strategy, in case they had not used this strategy spontaneously during the learning process. That is, we were interested in whether children would be successful on this task immediately, which would suggest that, similar to adults, they had processed the sequential egocentric and the allocentric strategies in parallel. If children do not succeed right away, it would be of interest whether children were able to learn to use the allocentric strategy.

5.2 Method

5.2.1. Participants

Seventy-seven children from 5 to 10 years of age, who were recruited from an elementary school situated in the Netherlands, participated in the study. Twenty children were excluded from the analyses: in the group of 5-year-olds only those children were included who learned the training route themselves (n = 7) or who, after the third trial, were shown the correct route by the experimenter and thereafter learned the route in a maximum of two trials (n = 10); in each of the group of 7-year-olds and the group of 10-year-olds two children were excluded due to concentration problems. The children who were included in the analyses were divided in three age groups: 5-year-olds (n = 17, number of girls = 9; mean age = 5.4, *SD* = 0.09 years), 7-year-olds (n = 19, number of girls = 7; mean age = 7.3, *SD* = 0.09 years) and 10-year-olds (n = 21, number of girls = 10; mean age = 10.7, *SD* = 0.07 years). The mean ages of both sexes did not differ overall ($p>.05$), nor did they differ within the different age groups (all groups, $p>.05$). The parents of the children gave consent for their child's participation. All participants reported to be healthy, had normal or corrected to normal vision and were unaware of the rationale of the study. The study was approved by the ethic committee of Utrecht University.

5.2.2. Apparatus and Stimuli

The Virtual StarMaze task has been successfully used in a study investigating adults' spontaneous strategy use during navigation (see Igloi et al., *submitted* for program details). The task was designed after a real life 'multiple strategies version of the StarMaze' in which mice were tested on their navigation behavior (Rondi-Reig et al., 2006). The maze consisted of five alleys forming a central pentagon and five alleys radiating from the angles of the pentagon, see Figure 1. The maze was surrounded by distal environmental landmarks for orientation; two different types of mountains, two distinct types of forests and two different antennas. In order to discourage the use of a guidance strategy, (non-identical) duplicates of landmarks were provided. Participants explored the maze in a first-person perspective, navigating through it by using a joystick (Logitech Attack 3 ®), which could move forward, backward and rotate in all directions. Before actual testing, participants practiced with handling the joystick until they understood how it worked, therefore practice time differed between the participants. The task was presented on a high-resolution 17-inch computer.

5.2.3. Design and Procedure

Participants received two versions of the StarMaze task, first the multiple strategies version, followed by the allocentric version. In the multiple strategies version, it could be examined whether and, if so, in which phase(s) of the learning process participants had spontaneously used a specific strategy; sequential egocentric, allocentric, corrected or a serial strategy. The allocentric version of the task, on the other hand, investigated participants' capability to use an allocentric strategy, in case they had not used this strategy spontaneously during the learning process.

Participants were instructed to navigate through the maze in order to find a hidden goal (a 'treasure' which consisted of a sparkling "bravo"), which would only appear if they were in the correct location in the maze. On each trial a maximum search time of 120s was allowed. If participants failed to reach the goal within the 120s they proceeded to the next trial. An exception involved the first three training trials: on these trials, if participants failed to reach the goal within 120s, they were placed in the goal alley and told to go straight ahead in order to reach the goal.

The multiple strategies version of the task, designed to identify spontaneous strategy usage, consisted of fifteen training trials and four probe trials regularly inserted between these training trials, see Figure 2D. Importantly, participants were not informed about the existence of the probe trials. In all the training trials, participants started at the end of alley 1 and had to find the goal which was located at the end of alley 7. After the first trial, participants could use different strategies in order to find back the goal: i) a sequence of successive turns (sequential egocentric strategy), ii) use the configuration of the environmental landmarks (allocentric strategy) or iii) successively enter each alley of the maze (serial strategy). In the probe trials, participants started from a different departure point (alley 5), however, the view on the surrounding landmarks was very similar to the view from the original starting point in alley 1 (compare Figure 1A with Figure 1B). This was also the case for the goal location. This way, at the beginning of the probe trials, participants did not directly notice that the departure point was different and were therefore triggered to use the same strategy as during the training trials. In the probe trials, and different from the training trials, participants were rewarded if using any of the strategies described above. That is, the sparkling “bravo” now appeared if participants navigated to the end of alley 1 (sequential egocentric strategy) as well as to the end of alley 7 (allocentric strategy). For the layout of the maze with the routes for the training and the probe trials, see Figure 1.

After participants had completed this multiple strategies version of the task, they received the allocentric version of the task which consisted of six trials. Participants were told in advance that they would start from a different departure point (i.e. the alleys that were not used previously: alley 3 and 9, Figure 1C). They were not explicitly instructed to search for (a specific configuration of) landmarks. However, now only alley 7 (goal location of the training trials) was rewarded, hence participants would only succeed if they used the environmental landmarks, and thus employed an allocentric strategy.

After completion of the multiple strategies and the allocentric version of the task, participants were asked to choose the correct layout of the maze, see Figure 5A for the six alternatives. They were shown the right layout and, provided with the start location, asked to draw the route they had taken to the goal location. Thereafter, participants were asked two questions: what they had seen in the environment and what strategy they had used.

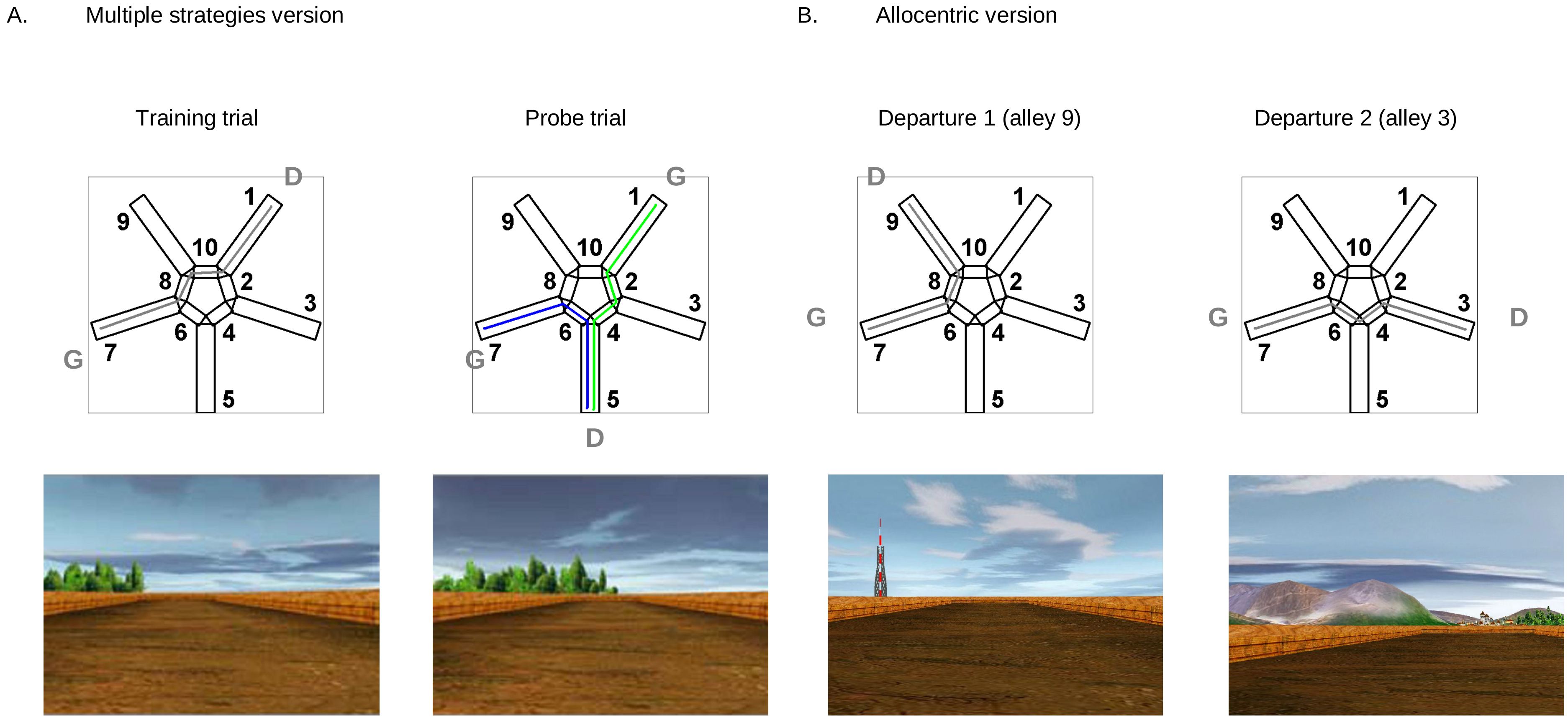


Figure 1. The Virtual StarMaze paradigm. **A** The multiple strategies version. The training trial: The departure point for the training trials was located at the end of alley 1 and the goal was located at the end of alley 7. In order to learn this path, participants could use an allocentric or a sequential egocentric strategy. Below, the view from the departure point of the training trial is represented. The probe trial: To identify which strategy participants had used to reach the goal, the departure point was changed to alley 5. The participant could use: i) the distal environmental cues corresponding to an allocentric strategy or ii) the same sequence of body-movements as during training trials (right-left-right body rotations) using a sequential egocentric strategy leading to the goal in alley 1. Both goal locations were rewarded on the probe trials. Below, the view from the departure point of a probe trial is shown. **B** The allocentric strategy version: Participants started from the ends of the alleys of the maze they had not yet departed from (alleys 3 and 9) and had to navigate to the goal located in alley 7. Below the views from the departure alleys of the allocentric version.

5.3 Results

5.3.1. Data Analysis

During each trial, participants exact position in the maze was recorded in a Cartesian coordinate system every 200 ms. From these records, the following parameters were calculated for each trial: the number of visited alleys (including the departure alley, all visited central alleys, the peripheral alleys that did not contain the goal and the goal alley), the total distance travelled from which the distance error (DE) was calculated, the mean speed, and the performed angles, that is the sum of absolute angles made with the joystick (PA) with which the measure performed rotations (PRs) was calculated.

The distance error (DE) is a normalized performance score (Igloi et al., *submitted*), for which the following formula was used: 100% x (total distance travelled – correct distance) / correct distance. The correct distance was similar to the ideal path length. A score of 0% corresponded to the correct distance and a value above 0% corresponded to a greater distance travelled compared to the ideal path length. The performed rotations (PRs) measure was calculated by subtracting the minimal amount of angles necessary to reach the goal via the ideal path (MA) from the sum of absolute angles made with the joystick (PA): PRs (º) = PA – MA. The greater the PRs value, the more participants had 'looked around' in the environment by making turns with the joystick.

Multiple strategies version

5.3.2. Performance parameters: number of visited alleys, DE, mean speed and PR

Figure 2 presents the number of visited alleys, the DE and the mean speed as a function of training trials for the three age groups. Visual inspection of the figure shows that participants performed well, and learned the task rapidly, though differences between the age groups can be observed. Five-year-olds reached a stable performance after the tenth training trial, 7-year-olds after the seventh training trial and the 10-year-olds after the fourth training trial. For the measure mean speed a significant difference was found for the factor Group, F (2,51) = 3.30, p < .05. Post hoc comparisons (Bonferonni corrected) showed that the 10-year-olds (147,6) differed significantly in mean speed from the 5-year-olds (134,1). For the other parameters no significant group differences were found: number of visited alleys, F (2,51) = 0.83, p = .44; DE, F (2,51) = 1.30, p = .28 and PRs, F (2,51) = 0.16, p = .85.

5.3.3. Strategies used measured by the probe trials

The four probe trials, in which participants were triggered to use the same strategy as they had used during the training trials, were regularly inserted between the fifteen training trials. The strategies, described in more detail in the method section, consisted of a sequential egocentric strategy, an allocentric strategy, a corrected strategy and a serial strategy. Participants who had used only one specific strategy during the four probe trials were called egocentric, allocentric, corrected or serial strategy users. Participants, on the other hand, who had used more than one kind of strategy on the probe trials, were classified as 'switchers'. Switches between strategies in different directions were observed. In Figure 3A.B the overall strategy used across probe trials is shown for each age group. In Figure 3B, the amount of rotations is shown per strategy and for each age group. Interestingly, it seemed that only the 10-year-olds (and not the 7-year-olds) who used an allocentric strategy showed an increase in amount of rotations at the beginning of the trial. However, since the amount of children spontaneously using an egocentric strategy was significantly higher than the amount of children using an allocentric strategy, it could not be reliably tested whether this increase in rotations was statistically significant.

Allocentric version

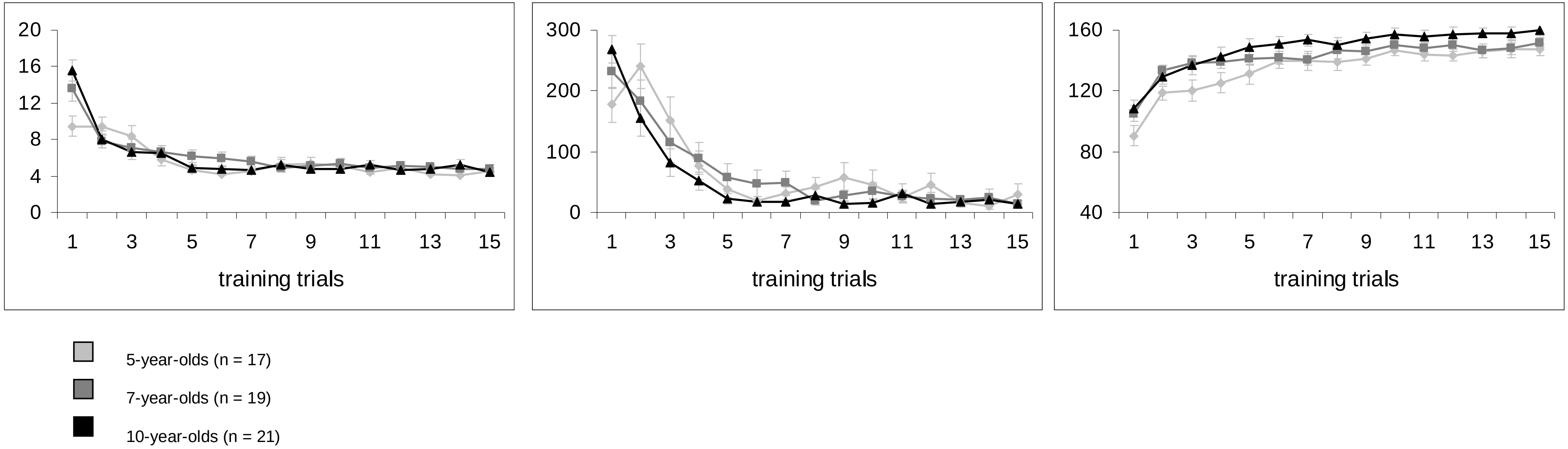
5.3.4. Performance parameters: number of visited alleys, DE, mean speed and PR

Despite the different strategies used in the multiple strategies version, all age groups performed above chance level (which is 25%, since in principle four alleys could contain the goal location) on the allocentric version of the task. Importantly, this was even the case for the children who exclusively had used an egocentric strategy across the probe trials. In trial number 1, 3 and 6 participants started from alley 9, and had to visit three alleys in order to find the goal. In the other trials participants started from alley 3, and had to visit four alleys to reach the goal. Overall, participants performed better on these latter trials (2, 4, and 5). This was statistically verified by post hoc repeated measures ANOVA with Departure point (2) as within-subjects factor and Group (3) as the between-subjects factor. This analysis yielded significant main effects for the factor Departure point for the following measures: number of visited alleys, F (1,47) = 20.81, p < .001; DE, F (1,47) = 11.43, p = < .01; mean speed, F (1,47) = 21.80, p = < .001 and PRs, F (1,47) = 24.76, p < .0001. Similar to participants' performance on the training trials, a Group effect was found for the measure mean speed (F (2,47) = 3.37, p = < .05). However, on these allocentric trials the 5-year-olds (127,7) differed from the 7-year-olds (141,7), with the latter being slower. None of the parameters showed a significant interaction effect between Group and Departure point (*p's* > .05). Figure 4 shows the amount of rotations for the two departure points for each age group. In each group, participants oriented themselves better at the beginning of the trials when departing from alley 9 compared to alley 3, however this effect was only statistically significant for the 10-year-olds (t (19) = 3.76, p < .001), and not the 5 and 7-year-olds (*p*'s > .05).

A Number of visited alleys

B Distance error (DE)

C Mean Speed

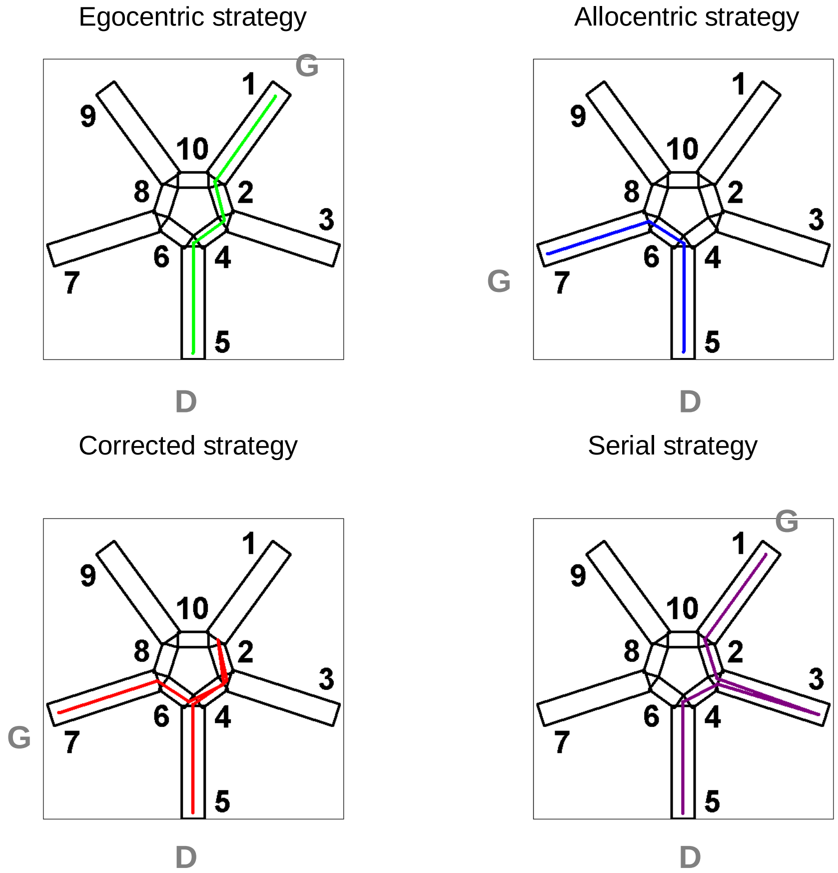


D

Tt1 - Tt2 - Tt3 - Tt4 - Tt5 - Tt6 - Tt7 - **Pt1 -** Tt8 - Tt9 - Tt10 **- Pt2 -** Tt11 - Tt12 - Tt13 **- Pt3 -** Tt14 - Tt15 **- Pt4**

Figure 2. The training trials. Performance parameters (number of visited alleys, percentage of distance error [DE]) and mean speed for the three different age groups. **A** Learning curve for the number of visited alleys; a plateau is reached after training trial 5. The number of visited alleys included departure, all visited central and peripheral alleys and the goal alley. Therefore, 4 is the minimum number of alleys to visit to get to the goal (alleys 1-10-8-7). **B** Learning curve for the percentage of DE; again a plateau is reached after training trial 5. **C** Mean speed of navigation during training trials; a plateau is reached after five trials. **D** Succession of training trials (Tt) and probe trials (Pt); each participant performed 15 training trials and four probe trials.

A Different strategies



B Strategies across the four probe trials per age group

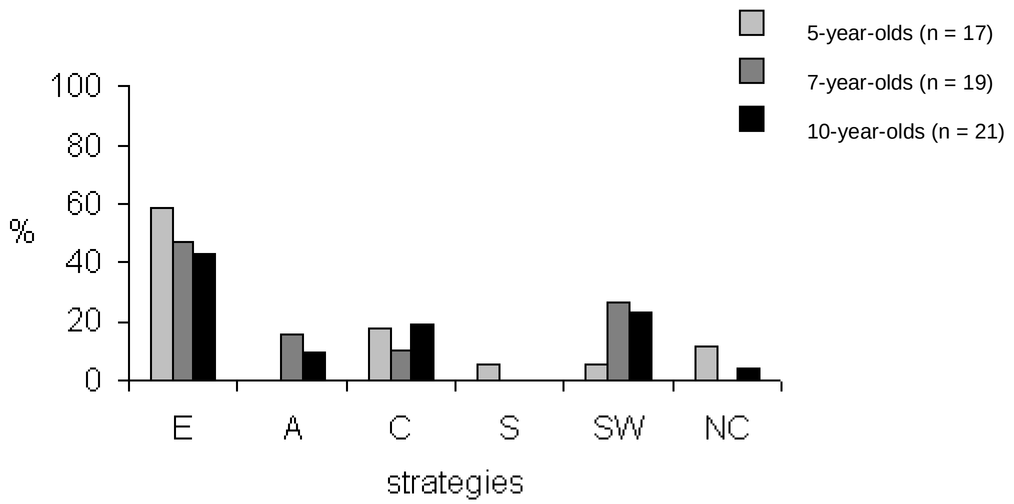


Figure 3A. The probe trials. **A** Four different strategies were used by the participants. From left to right: i) allocentric strategy. ii) sequential egocentric strategy. iii) corrected strategy. iiii) serial strategy. **B** The overall strategy used across the four probe trials for the three age groups; E = sequential egocentric strategy, A = allocentric strategy, C = corrected strategy, S = serial strategy, SW = switches between strategies on the four probe trials, NC = no clear strategy.

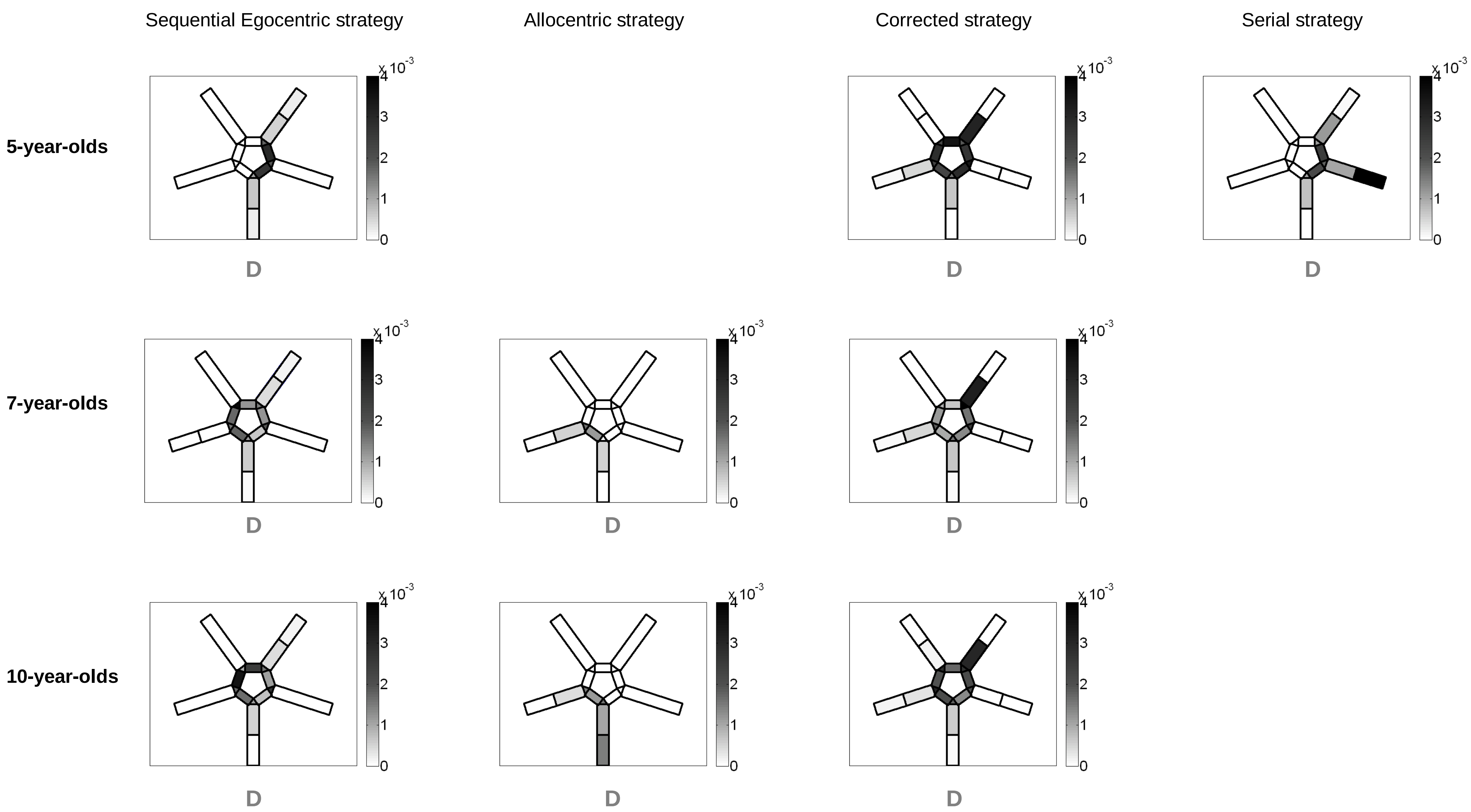


Figure 3B. The probe trials. The amount of rotations performed in different parts of the maze presented per strategy used across the four probe trials for the three age groups.

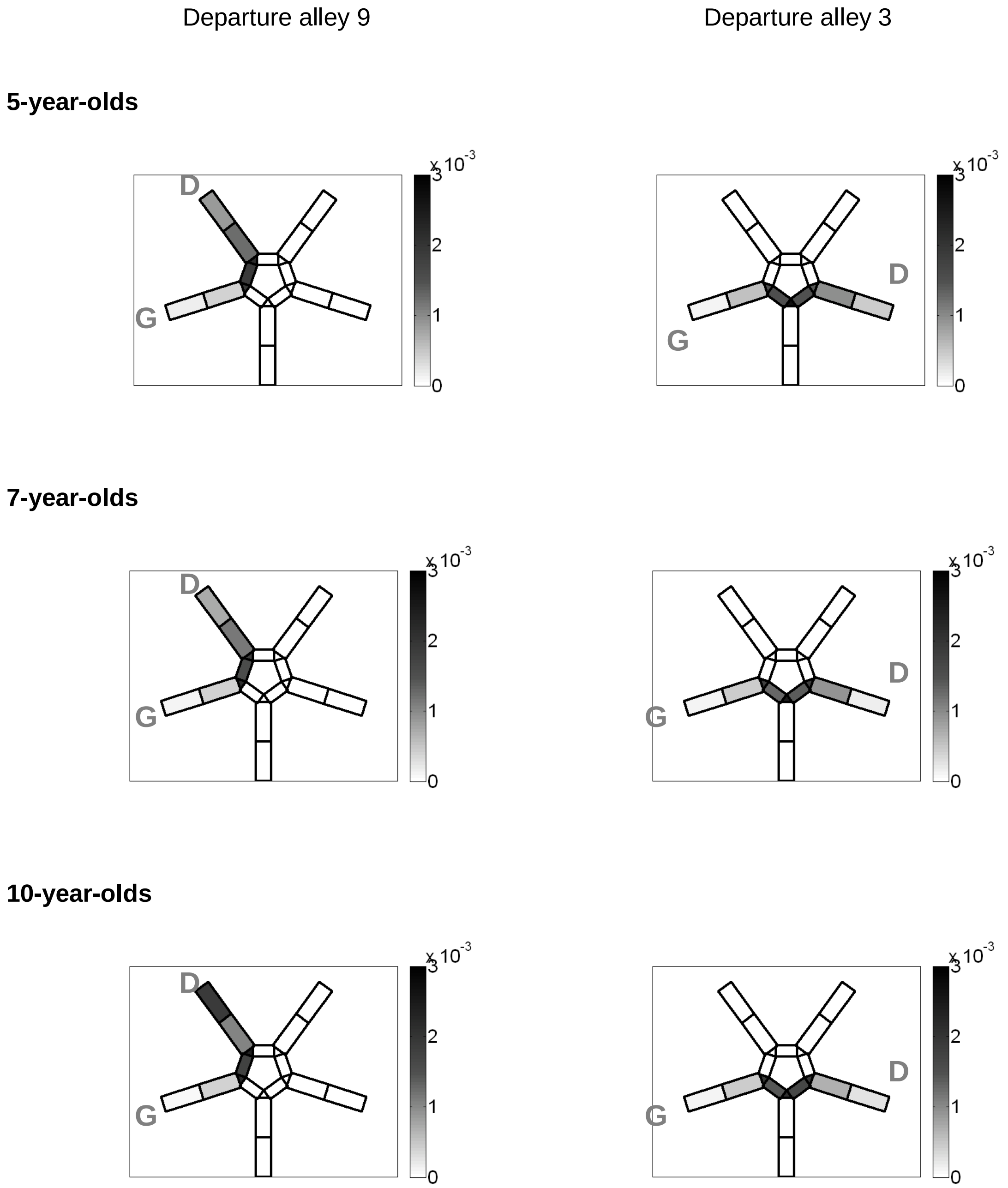


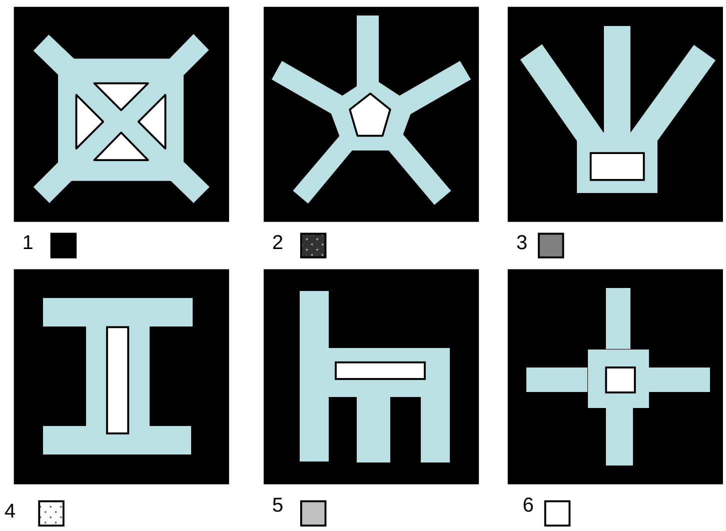
Figure 4. The allocentric trials. The amount of rotations performed in different parts of the maze presented for the two departure points (alley 3 and alley 9) and all three age groups. In trial number 1, 3 and 6 participants started from alley 9, and had to visit three alleys in order to find the goal. In the other trials participants started from alley 3, and had to visit four alleys to reach the goal.

5.3.5. Additional tasks

After completion of both task versions, participants were asked to choose the correct layout of the maze. In Figure 5B participants' choices are presented. The figure shows that the oldest children, the 10-year-olds performed best: 61% of the children in this age group chose the correct layout of the maze, compared with 16% of the 7-year-olds and 13% of the 5-year-olds, which are both close to chance level (17%). The children were also asked to draw the route from the start to the goal location, thus from alley 1 to alley 7. Again, the oldest children were best at this task, with 86% of the children drawing the correct route, compared to 63% of the 7-year-olds and 38% of 5-year-olds reproducing the exact route.

All children verbally reported to have noticed the environmental landmarks, and were able to name several of them. Some children, especially the younger ones, had difficulties with explaining the strategy they had used, but others could explain well that they; 'paid attention to the mountains and/or trees or village' (allocentric strategy), 'remembered the route', and some of the children even reproduced the right-left-right route (sequential egocentric strategy) or a combination of both strategies (corrected strategy). When asked for, almost all children who exclusively had used a sequential egocentric strategy in the multiple strategies version, were able to explain the strategic difference between this version and the allocentric version of the task.

A



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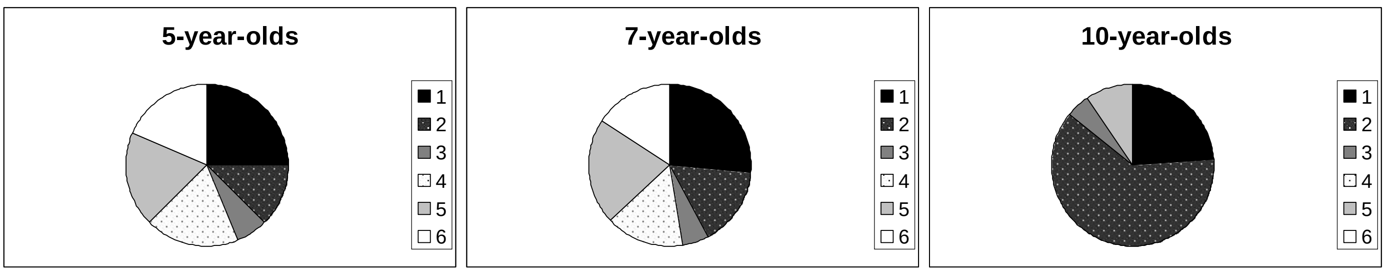

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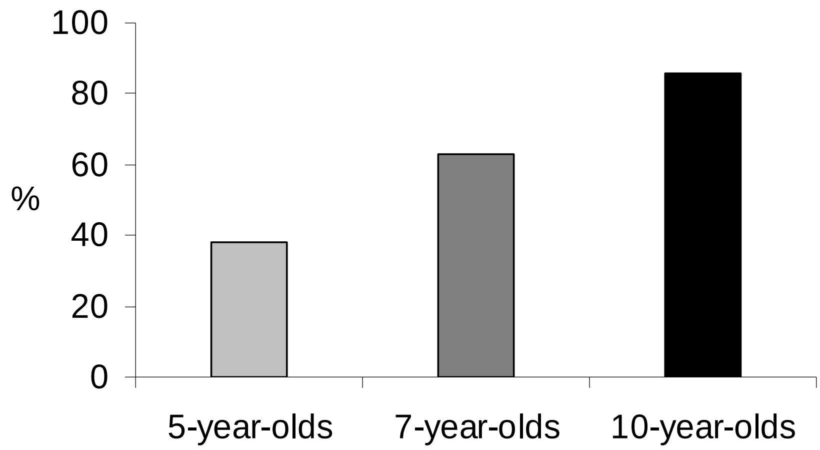

Figure 5. **A** Six alternatives from which participants could choose the correct layout of the maze. **B** Charts with percentages of layouts chosen by the participants in the three age groups. The 5 and 7-year-olds performed at chance level when asked to recognize the maze. Only the 10-year-olds were able to correctly recognize the layout of the maze. **C** The percentage of correctly drawn routes for each age group.

5.4 Discussion

In the present study children aged 5, 7 and 10 years were tested on the virtual StarMaze task (Igloi et al., *submitted*; Rondi-Reig et al., 2006). This task measures participants' spontaneous use of strategies during navigation. Two versions of the task were assessed: the multiple strategies version and the allocentric version. In the training trials of the multiple strategies version, participants had to learn a fixed route to a goal. In the intermixed probe trials the departure point changed unbeknownst to the participants. Since the views from the departure points in the training trials and in the probe trials were highly similar, participants were encouraged to use the same strategy as they had used during training trials. In the probe trials both the use of a sequential egocentric strategy in which participants encoded the sequence of body turns as well as the allocentric navigation strategy in which participants encoded the configuration of environmental landmarks were rewarded. In the allocentric version, participants again started at a different departure point; however, in this case the starting view was dissimilar to the view in the training trials. Importantly, in this version of the task the only strategy that was rewarded was the allocentric strategy. It was hypothesized that the sequential egocentric and as well as the allocentric strategy depend on the (left) hippocampus, and are therefore proposed to appear early in training (Iaria et al., 2003; Iglói et al., *submitted*; Poldrack et al., 2001). Given that they might provide insight on the structural or functional development of hippocampus, we were interested in children's spontaneous use or their ability to use these navigation strategies at a certain stage in the learning process.

First, it is important to note that almost half of the 5-year-olds had difficulties with the task demands, only the children who managed to learn the training route themselves or were helped in the very beginning of the task were included in the analyses. All age group showed good performance on the training trials. Except for the mean speed parameter, and the fact that each age group reached a stable performance at different times in training, no overall significant group effects were found for participants' performance on the training trials. Thus although the mean speed of the youngest age group was significantly lower on the training trials compared to the oldest children, the age groups did not differ in number of visited alleys, in distance error or in amount of performed rotations. This means that potential differences between the age groups on the probe trials, in which spontaneous strategy use (i.e. sequential egocentric strategy, allocentric strategy, corrected strategy or serial strategy) was measured, cannot be explained by their overall performance on the training trials.

For the probe trials, it was apparent that none of the 5-year-olds had solely used an allocentric strategy, though two children did show a corrected strategy, starting off in an egocentric way and 'correcting' themselves along the route by using the surrounding environmental landmarks (i.e. allocentric strategy). This young children's preference for an egocentric strategy is in accordance with egocentric spatial updating being observed at a young age (Nardini et al., 2006), whereas the use of environmental landmarks for location coding and navigation appears later (Newcombe & Huttenlocher, 2000). All age groups, like the adults described by Igloi and colleagues (*submitted*) showed switches of strategies between the probe trials in different directions early in training. This finding might indicate that, at 5 years, the hippocampus, i.e. the neural structure involved in both navigation strategies, is structurally mature. In addition, the fact that, in specific, age differences were observed in the use of an allocentric strategy, might indicate that the hippocampus matures functionally over the years (Overman et al., 1996). This functional maturation of the hippocampus during primary school, is possibly stimulated by extended navigation experience. That is, developmental changes in navigation might depend on a combination of biological maturation, on experience with certain information sources, and/or on their (possibly bi-directional) interaction (Newcombe et al., 1998). Imaging studies with children might provide further insight in this matter (Overman et al., 1996).

Furthermore, it should be noted that, although, the performance of 7 and 10-year-old children was similar to that of adults, differences exist between how the child groups oriented themselves in the environment. For the allocentric strategy used during probe trials, 10-year-olds oriented with respect to the environmental landmarks at the beginning of each trial. The 7-year-old children, on the other hand, did not show this orientation behaviour, though they still showed a direct allocentric strategy. How is this possible? The answer should be sought in participants' performance on the training trials. All of the 7-year-olds who had used an allocentric strategy across the probe trials had learned a different route on the training trials, that is instead of going right-left-right they had used a left-right-right-left sequence to find the goal location. Therefore, on the probe trials, it might be possible that, on their way, they had recognized the environmental landmarks that were close to the goal location. Although this might also have been the case for one of the 10-year-olds, the difference in rotation patterns indicates different orientation behaviours. In all, the 7 and 10-year-olds did show a spontaneous use of landmarks (i.e. allocentric strategy), while the 5-year-olds did not.

For the allocentric version, even on the first trial, all age groups performed above chance level. This finding indicated that, although none of the 5-year-olds had spontaneously used an allocentric strategy on the probe trials, it can be concluded that they had acquired this strategy in parallel to their preferred sequential egocentric strategy (Burgess, 2008; Nadel & Hardt, 2004). The same was true for the older children. For all age groups, even in case of a sequential egocentric strategy, direct paths to the goal location were observed. The use of an indirect path indicated that participants had oriented themselves along the way. Interestingly, across age an effect was found for departure point: children performed better when they departed at the end of alley 3, from which they could easily see the configuration of landmarks that were close to the goal location. In the other case (departure starting from alley 9), participants first had to orient themselves. Comparable to their orientation behaviour for the allocentric strategy used during probe trials, the 10-year-old children were the only ones who showed orientation behaviour at the beginning of the path. In contrast, the younger children oriented themselves along the way. Thus, although all children had used the landmarks (in some cases parallel to a sequence of body turns) to find the goal location, performance on both probe and allocentric trials showed that the age groups used different strategies to orient themselves in the environment.

With respect to the additional tasks provided at the end of the testing session, only the 10-year-olds performed above chance level when asked to recognize the maze. This means that they not only had oriented themselves differently than the younger children, they had also created an explicit cognitive representation of the maze during completion of the task. Whether they actively used this representation to solve the task cannot be ascertained here. The fact that the younger children did not recognize the layout of the maze, could either mean that they were not able to build a cognitive representation of the maze during the task, or that they had difficulties with mapping it onto a two dimensional format (Nardini, 2006; May, 2004). In addition, it was shown that, although all children had less difficulties with drawing the route than with choosing the correct layout, again the 10-year-olds were best at drawing the correct route in the maze.

In conclusion, it was demonstrated that 10-year-old children oriented themselves differently in the environment than younger children did. The oldest age groups oriented at the beginning of a path, before starting to walk, whereas the younger children oriented themselves with respect to the environmental landmarks during the route. In addition to this age difference, it was shown that children 5 to 10 years show similar use of navigation strategies compared to adults. That is, behavioral evidence was given for the use of allocentric and sequential egocentric strategies at an early stage in training in both children and adults. We take this as indirect evidence for the fact that the hippocampus might be structurally mature at already the age of 5 years. Differences in the preference for certain strategies might indicate further functional maturation of the hippocampus during primary school age (Overman et al., 1996).

CHAPTER 6

THE EFFECT OF FEEDBACK ON CHILDREN'S ABILITY TO SHOW REPONSE AND PLACE LEARNING

Bullens, J., Székely, E., Vedder, A. & Postma, A. The effect of feedback on children's ability to show response and place learning. (*submitted for publication*)

Abstract

From a developmental perspective, it has been reasoned that, over the course of development, children make differential use of available landmarks in the surroundings to orient in space. The present study examined whether children can learn to apply different spatial strategies, focusing on different landmark cues. Children aged 7 and 10 years were tested on an object-location memory task in which they learned a location relative to a local cue or to distal cues. Both age groups performed equally well on the local test condition. Children 7 years of age had difficulties with orientating relative to distal landmarks. However, when provided with feedback, performance increased significantly. Two explanations could account for the findings: a delayed maturation of the hippocampal function and/or experience with the use of distal landmarks for coding location.

6.1 Introduction

In order to reorient in a successful manner, all moving species must somehow create an internalised representation of their surroundings. In humans it has been shown that mental representations are based on at least two different types of features of the environment, i.e. geometric and non-geometric features. When orienting, humans make use of the shape of the environment (geometric feature) in combination with available landmarks (non-geometric features). In the literature concerning the development of spatial cognition it has been debated whether children possess an encapsulated ‘geometric module’ (similar to for example rats) through which they (re)orient in space (Wang and Spelke, 2002; Wang et al., 1999; Hermer & Spelke, 1996; 1994). However, Learmonth and her collaborates (2002, 2001) suggested that this phenomenon should not be viewed as a ‘module’ for reorientation, given that children in the same age range, when tested in a larger testing space, were able to use geometry of the room in combination with salient landmark cues, depending on easiness of movement and distance to the landmark (Hupbach & Nadel, 2005 and see Learmonth et al., 2008 for a review). In fact, studies investigating the development of orientation behaviour have confirmed that young children are specifically capable of learning their own or an object’s location relative to a single landmark (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003).

In general, a distinction can be made between two kinds of landmarks of which each is typically involved in a different type of learning; local landmarks in *response* learning and distal landmarks in *place* learning. Learning responses to an individual landmark of which its location is contiguous to the goal of navigation (i.e. local landmark) (or learning a specific sequence of motor movements) is called *response* learning. *Place* learning, on the other hand, involves the ability to build a representation of the environment with the use of distal landmarks (i.e. objects further away from the goal) and/or the geometry of the environment (O’Keefe & Nadel, 1978; Overman et al., 1996; Packard & McGaugh, 1992, 1996; Tolman et al., 1946; White & McDonald, 2002). Importantly, it has been suggested that within spatial memory these two types of learning can be dissociated in terms of their developmental trajectories (Akers & Hamilton, 2007). Memory for spatial locations seems to improve systematically with age (Huttenlocher et al., 1994; Newcombe & Huttenlocher, 2000), with *response* learning developing first followed by *place* learning. *Place* learning is first observed around 21 months of age (Newcombe et al., 1998) and continues to develop into the school years (Newcombe et al., 2007).

A task specifically designed to test the emergence of spatial *place* learning in children is the Kiel Locomotor Maze (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003). This task consists of a circular environment with experimentally controlled local and distal cues, in which participants of different ages had to search for hidden locations (Lehnung et al., 1998). During the experiment, the configuration of the maze was changed so that the two cues (local and distal) were placed in conflict. Participants’ responses indicated which cue types they were spontaneously using. It was consistently shown that young children 3 to 5 years of age, compared to older children (8 to 10 years), had difficulties with basing their searching behaviour on the distal cues (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003). In the present study we were interested in children’s ability to learn to use different cues with the help of feedback, instead of children’s spontaneous use of different cue types. That is, do 7 and 10-year-old children profit from feedback when they have to learn to associate an object's location with a specific type of cue?

To our knowledge, up to this point only one study did examine the actual learning patterns of young children on a place strategy task (Overman et al., 1996). Following the example of previous studies on place learning in rodents (Hamilton et al, 2007; 2008; Pearce et al., 1998) employing the Morris water maze (Morris, 1981), children learned the location of a treasure box in a pool filled with plastic chips. They were only able to succeed if they learnt the location of the box in relation to the distal cues, i.e. pictures that were attached to a floor-to-ceiling curtain, surrounding the pool. No local cues were available in this task. Participants in different age groups were given several search trials across three consecutive days. On the third day of testing, the distal cues on the curtain surrounding the pool were removed. It was found that children older than 7 years of age generally performed better than younger children, suggesting that place learning does not fully mature until the age of 8 years (Overman et al., 1996). However, an apparent finding that might challenge this conclusion was the fact that all children improved in performance from the second to the third test day. This would mean that the distal cues did not actually help the children in learning about the correct location. Alternatively, the researchers suggested that the children either had used different external cues outside the search space or they had used the entrance of the experimental space as a reference point, which would imply the use of a response strategy. Disorientating the participants after they had entered the testing environment could have eliminated these possibilities.

In the present study, we investigated the extent to which the development of different spatial learning strategies is dependent on an increment in relevant experience and the ability to learn from these experiences. Children aged 7 and 10 years were tested on an object location memory task in which they were required either to learn a location relative to a local cue (*local* test condition measuring response learning) or to learn a location in relation to distal cues (*distal* test condition measuring place learning). The learning patterns of the children not only provide insight into their abilities to show response and/or place learning, but also give insight to what extent they are able to profit from feedback and thereby improving their performance on any of the learning strategies. In line with the idea that 7-year-old children are in a transitional age for place learning (Lehnung et al., 1998), we hypothesized that the learning patterns of the children in this age group in the *distal* condition would differ markedly from the 7-year-olds in the *local* test condition and the 10-year-olds in both test conditions. We measured children's radial distance errors and angular error, and expected the 7-year-olds to show large angular errors in the *distal* test condition, but not in the *local* test condition.

6.2 Method

6.2.1. Participants

Ninety-four children (47 girls) from two Hungarian primary schools and one German primary school participated in the study. The children were divided in a group of 7-year-olds (mean = 7.5; SD = .39) and a group of 10-year-olds (mean = 10.5; SD = .31). None of the children were known to have any neurological or psychiatric disorders and/or perceptual impairments. All parents gave consent for their child's participation. Having completed the task, children received a small present for their participation. Within both age groups, an equal number of boys and girls were randomly assigned to the *local* and to the *distal* condition.

6.2.2. Apparatus and Stimuli

The circular experimental space (3.2m in diameter) in which the children were tested comprised six pieces of identical wooden room separators, each 1.4m x 1.6m. The wooden panels were held together by velcro. In order to prevent children from taking advantage of the location of the velcro a blue non-transparent cotton fabric (1.4 x 10m) covered the inner surface of the panels. The floor inside the experimental space was fully covered with homogenous black cotton fabric. A smaller blue round carpet measuring 1.6m in diameter indicated the 'active' search-area on the floor, see Figure 1 for the experimental set-up. Three laminated pictures, each depicting a different underwater world scene (color print, size A4), acted as distal cues. Each pictures' frame had a different color to increase their uniqueness as a cue. They were attached to the blue fabric on the wall in the middle of every second panel, at eye level for the children. The local cue, placed on top of the blue round carpet, consisted of a laminated color picture of a sea shell (size 9 x 7cm) and the target object was either a laminated color picture of a clown fish or of a turtle (size 8,5 x 6cm). The local cue was always placed on the carpet with a radius of 60cm from the center of the carpet. Both possible target objects were pictures of characters from the animation movie 'Finding Nemo' of Pixar distributed by Walt Disney Pictures. Several A1-sized black carton papers were used to cover the view above the wooden panels. The experimenters made sure that no external sources of light and sound could be used as possible (distal) cues. One of the six wooden panels also functioned as entrance to the experimental space. Having entered the test-arena, the blue fabric was secured again to the adjacent panel with velcro on the back side.

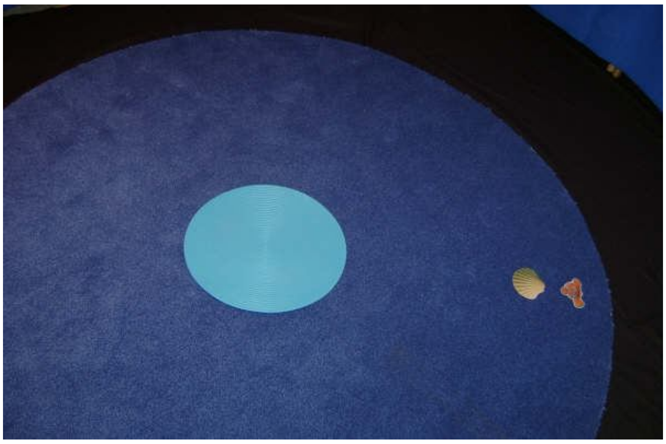

Figure 1. Experimental set-up showing the active search-area with the local cue (sea shell) and the target object (in this case a laminated color picture of a clown fish) placed on top of the carpet.

6.2.3. Design

The children were randomly assigned to either the *local* or to the *distal* test condition. Both test conditions consisted of two consecutive blocks of six trials each. In every trial the local cue was moved to one of the six predefined locations in the 'active' experimental space (on top of the blue round carpet) in quasi random order. Thus the local cue remained visible on the carpet in both conditions during the experiment. It was the participant's task to memorize the location of the target object. In the local test condition, this target object remained in a constant distance and direction relative to the local cue (sea shell) which was moved to a new place before every trial. In the *distal* condition, on the other hand, the target object remained at a fixed location throughout an experimental block in a way that only the distal cues could provide the correct information about the target location. In the local test condition it was the local cue that indicated the object's location. Within each condition, the block sequence, as well as the identity of the target object, was counter-balanced across subjects. In one of the two experimental blocks the center of the object was always 10cm exactly below the center of the local cue while in the other block the object was placed 10cm to the bottom right from the local cue, while the local cue kept its orientation constant (as indicated by its internal axis). For the *distal* condition, the object was either exactly in line with and underneath a distal cue, or exactly in between two distal cues. The distal cues were the same for all children.

6.2.4. Procedure

After the participant and the experimenter had entered the test-area, the child was encouraged to explore the experimental space and the (potential) cues. The child was asked to name some random items depicted in the distal cue pictures and he/she was familiarized with the target objects and the local cue. The child was then instructed to step onto a light-blue spot located at the centre of the blue carpet. The experimenter placed the local cue and the target object on top of the carpet, and asked the child to remember the location of the target object. The experimenter assisted the child in turning around, with eyes closed, in alternating directions in order to disorient him/her. At the same time the experimenter silently walked around the child in different directions, in order to avoid becoming a directional cue to the child. The experimenter made sure that at the end of the rotations the child faced a different distal cue than at the beginning of the rotation procedure. Next, children had to count to 15 out loud with their eyes closed. During this time the experimenter placed the target object underneath the carpet at the indicated hiding location. This location was fixed in the *distal* condition, however, in the local test condition, from the second trial onwards, the object was moved to a new location together with the local cue keeping its predefined relation to the local cue. This procedure was repeated six times throughout a test block. Subsequently, the child was asked to open his/her eyes and to indicate where he/she thought the target object was hiding by placing an identical picture of the target object on top of the blue carpet. Afterwards, the experimenter always showed the child the correct location by lifting the carpet, and placing the target object from under it back on top of the carpet in the designated location. During the test trials the experimenter was constantly moving around in the 'passive' experimental space to prevent her from becoming a cue to the child. At the start of the second test block, a new target object was introduced to the child.

6.3 Results

Children's performance was measured by two error types indicating proximity to the target location; the angular error and the radial distance error. The angular error (in degrees) was the angle between the original target location and the response location to the centre of the active search-area. The radial distance error (cm) was the absolute difference between the correct distance of the target location to the centre of the search environment and the distance from the response location to the centre of the search environment. In order to control for the fact that children could perform correct by chance, we calculated standardized performance scores for the radial distance error with the following formula: performance score = 100 (chance distance – radial distance error) / chance distance. Chance distance was calculated as follows: $[2/3(R) – (r_s)] + [2/3 (r^3)/(R^2)]$, in which R is the radius of the search space and r_s is the radius of the stimulus (i.e. target object). Since the target object was, on average, located at a radius of 70cm from the center of the search space, chance distance was: $[2/3 (80cm) – (70cm)] + [2/3 (70cm)^3 / (80cm)^2]$, thus 19.1cm. Similarly, we calculated standardized performance scores for the angular error with the formula: performance score = 100 (chance angle – angular error) / chance angle. The angular error made by chance was 90 degrees. Following these transformations, a score of 100 indicates a correct search, whereas a score of 0 indicates chance performance. A score below 0 indicates an error greater than expected by chance.

Figure 2 and figure 3 respectively plot the angular errors and the radial distance errors for both age groups per test condition, shown by block for the six trials in each block. Both error types were subjected to a repeated measure ANOVA, with Block (2) and Trial (5) as the within-subjects factors and Group (4), created by age and condition, as the between-subjects factor. The first trials of both test blocks were excluded from the analyses since participants received feedback only after their first response, and therefore learning could only occur after the first trial. The results of the two analyses are discussed below. In an additional analysis, we checked whether the object's location relative to either of both cues (i.e. directly 'underneath' the local or distal cue vs. 'underneath and to the right' of the local cue or between two distal cues) had any effect on children's performance. Since no effect of location of the target object with respect to and/or distal cue(s) was found, we did not include location as an extra factor in the analyses. Thus possible effects caused by memory load (i.e. in the distal test condition remembering either one or two cues) differences between the test conditions are not observed. Also, we did not find any differential effects for boys and girls, therefore all data were collapsed across gender.

6.3.1. Angular errors

The repeated measures ANOVA with angular errors as dependent variable yielded several significant effects. Most importantly, in line with our expectations a Group effect was found (F (3,89) = 34.35, p < .001); post hoc comparisons (Bonferonni corrected) showed that the 7-year-old children in the *distal* test condition differed significantly in performance from all the other groups, see Figure 2. That is, overall these children made greater angular errors (39.8) than the 7-year-olds in the *local* test condition (89.8), the 10-year-olds in the *distal* test condition (79.7) and the 10-year-olds in the *local* test condition (87.0). Additionally, for both within-subjects factors Block (F (1,89) = 33.96, p < .001) and Trial (F (4,356) = 15.57, p < .001) a main effect was found. Participants showed a significant linear learning effect between blocks in that overall they performed better on the second (mean = 81.7) than on the first block (mean = 66.3). Besides, within test blocks performance linearly increased as well. Also, both factors significantly interacted with each other, F (4,356) = 3.77, p < .01. Two paired-samples T tests with adjusted alpha showed that participants' performance increased more significantly over trials in the first test block than in the second test block; 2nd to 6th trial in first test block, t (93) = 5.41, p < .001 and 2nd to 6th trial in the second test block, t (93) = 2.28, p < .05. From Figure 2 (and also Figure 4) it can be seen that the 7-year-olds in the *distal* test condition, performed at (or significantly close to) chance level on the second and third trial in the first test block. This visual impression was statistically verified by One-sample T tests with test values at 0; second trial, t (23) = 0.26, p > .05 and third trial, t (23) = 0.36, p > .05. Only from trial four onwards the 7-year-olds in this test condition performed significantly above chance level. Finally, a significant interaction effect was found for the factors Group and Block, F (3,89) = 4.64, p < .01. A post hoc one-way ANOVA (Bonferonni corrected) indicated that the 7-year-old children in the *distal* test condition differed more significantly from the other groups in the first test block (F (3) = 35.74, p < .001) than in the second test block (F (3) = 14.79, p < .001). Thus despite the fact that all groups showed a marked improvement between blocks, this improvement was relatively stronger for the 7-year-old children in the *distal* condition. This effect, however, does not seem to be surprising given that the other groups did not have much room for improvement in the second test block.

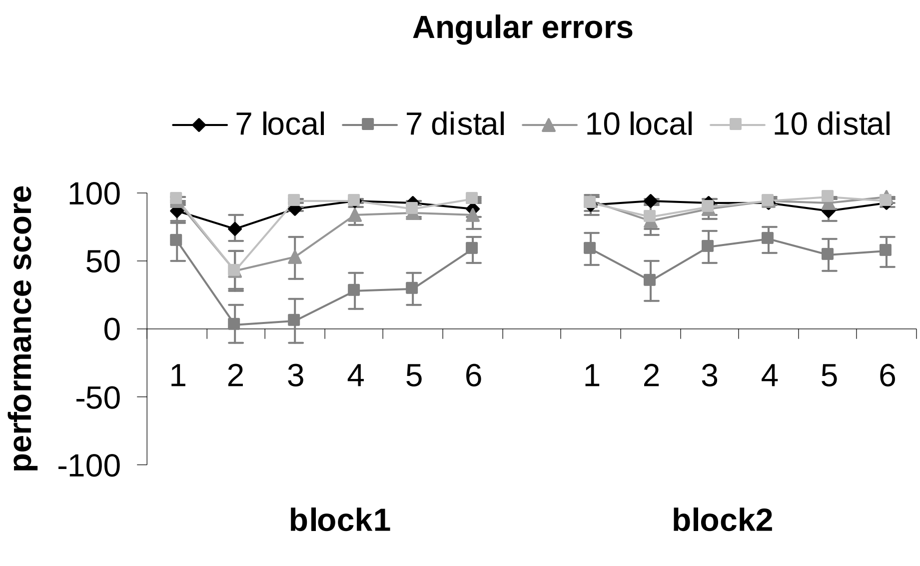

Figure 2. Performance scores for angular errors for both age groups per test condition, shown by block for the six trials in each block.

6.3.2. Radial distance errors

The second repeated measures ANOVA with radial distance errors as dependent variable also showed a significant Group effect (F (3,89) = 3.87, p < .05). However, this effect differed from the one described for the angular errors as a post hoc test (Bonferonni corrected) revealed that the two age groups differed significantly from each other in the local test condition with the 7-year-olds making significantly greater radial distance errors in this condition (mean = 67.7) than the 10-year-olds (mean = 85.1). Thus contrary to the analysis on angular errors, the 7-year-olds in the *distal* test condition did not differ from the other groups in the amount of radial errors, Figure 3. Furthermore, and similar to the angular error findings, a Block effect was found, F (1,89) = 16.16, p < .001, which again indicated that participants had learned between blocks (mean first block = 71.7 and mean second block = 79.2). Contrary to the angular error findings, however, no effect for the factor Trial was obtained, suggesting that overall (thus across test blocks) participants did not learn within a test block. On the other hand, a significant interaction effect between the factors Block and Trials was found, F (4,356) = 2.79, p < .05. Two paired-samples T tests with adjusted alpha demonstrated that participants' performance increased significantly over trials in the first test block, but not in the second test block; 2nd to 6th trial in first test block, t (93) = 3.60, p = .001 and 2nd to 6th trial in the second test block, t (93) = 0.15, p > .05.

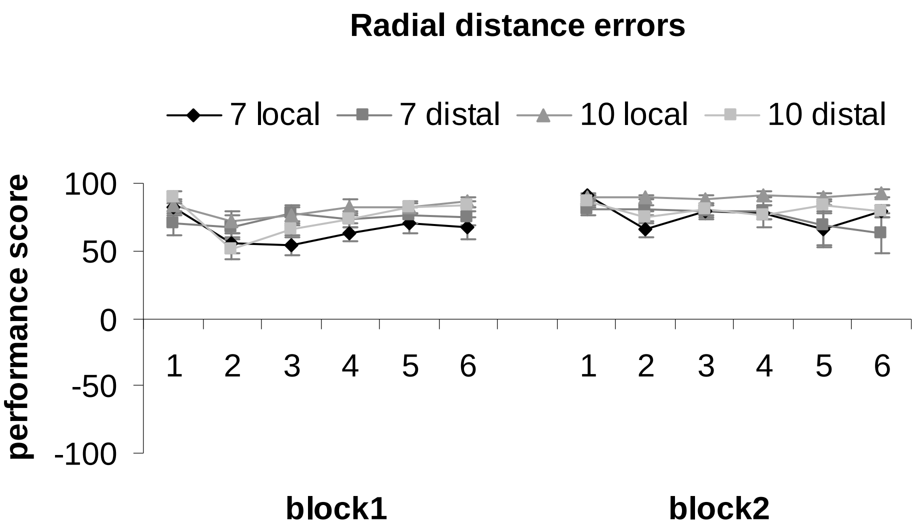

Figure 3. Performance scores for radial distance errors for both age groups per test condition, shown by block for the six trials in each block.

6.4 Discussion

In the current study, children 7 and 10 years of age were tested on an object location memory task, in which the ability to use different type of landmark cues was assessed. In the local cue condition, the target object was associated with the landmark and measured participants ability to show response learning. In the *distal* condition, the target object was related to the distal landmarks surrounding the maze and measured participants ability to show place learning. We were interested in what kind of information (i.e. landmarks) children in the different age groups were able to learn to use while orienting in the maze, thus whether they were able to profit from feedback. Two types of error measurements, angular errors and radial distance errors, were used in order to examine their effects on the learning patterns of children. First of all, it should be noted that children's overall performance was above chance level, showing that they had understood the instructions, and could adequately respond to them.

It was shown that, for the angular errors, 7 and 10-year-old children were able to profit from feedback to a dissimilar extent depending on whether they were tested in the *local* test condition or in the *distal* test condition. Seven-year-old children in the *distal* test condition performed significantly worse than 10-year-olds in this test condition and than both age groups in the *local* test condition. Interestingly, on the first trial of the experiment all children performed above chance level, whereas on the second and third trials the 7-year-olds in the distal test condition performed at chance level. On the first trial, participants could have used both the local cue as well as the distal cues for relocating the object. On the second trial, the local cue was moved for the first time, and probably the 7-year-olds in the distal test condition guessed that the object was related to it, since they performed at chance level compared to the 7-year-olds in the local test condition. Although they had received feedback after the second trial, children in this group still performed at chance level on the third trial. It was only after this trial that they understood that the object was associated with the distal cues. As shown in figure 2, performance increased over the rest of the trials. It was shown that, although spontaneously using the local cue, 7-year-old children are able to learn to use distal cues, without being explicitly told to do so. Importantly, seven-year-olds' worse performance on the distal test condition could not be ascribed to their perceptual incapability to compute angles, since the to-be-remembered angles were, on purpose, easy in use, either right underneath or "in between".

The analysis of the radial distance errors, on the other hand, did not reveal a group effect. This finding, however, does not necessarily suggest that the 7-year-olds had used the distal cues for this measurement. An alternative, and more plausible, explanation is that they had used the distance to the boundary of the search space (i.e. the circular carpet) as an indication for distance instead. Thus the 7-year-old children were able to take into account the radial distance of the target object to the centre (or boundary) of the search environment, but they had difficulties with orienting themselves with respect to the distal landmarks. Taken together, these findings corroborate and extend those reported elsewhere (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003) and supports the idea that 7-year-old children are bound to a response strategy and that they generally do not display a place strategy spontaneously. Importantly, this study is one of the first to show that, when provided with feedback, children are able to learn to use distal landmarks even before the age of 10 years.

Interestingly, visual inspection of the learning curves of the 7-year-olds in the *distal* condition showed that children did not benefit from their significant improvement in angular errors from the first to the second test block. Although the children performed better in the second test block compared to the first, it seems that, in the second test block children had reached their maximum level of learning (contrary to the floor effect shown by the other groups) which prevented them to further reduce their error rates. It can be concluded that, although 7-year-old children are able to profit from feedback, they can only do so to a certain extent. This could indicate that, although young children are able (to learn) to use distal cues to make a representation of the environment, in general, older children have better processing capacities to learn to an optimal extent (Sandberg, 1999).

Two explanations (or a combination) could account for this development in place learning. First, it has been proposed that the later emergence of place navigation depends on the delayed maturation of the hippocampal function (Overman et al., 1996), a neuro-anatomical structure that is often related to place learning (O’Keefe & Nadel, 1978). Although Pentland and colleagues (2003) pointed out that studies examining the structural development of the hippocampus do not suggest a critical period of development around the age of 7 or 8 (see also Lavanex et al., 2007), it might still be true that the hippocampus does develop functionally during this period. Additionally, at the age of 7, children become more experienced with autonomous wayfinding behaviour (i.e. walking or biking to school) and this could result in more efficient use of place strategies. Future research should shed more light on the tenability of (a combination of) both possibilities (Newcombe et al., 2007).

In conclusion, the findings of the current study give new insights in the development of spatial strategy use in children. We were able to show evidence for differences in the extent to which children in different age groups are able to learn to use specific types of landmarks for orientation. That is, compared to 10-year-old children, 7-year-olds had difficulties with orientation in relation to distal cues. However, when provided with feedback, their performance increased. Both age groups performed equally well on the local test condition in which they were required to show response learning.

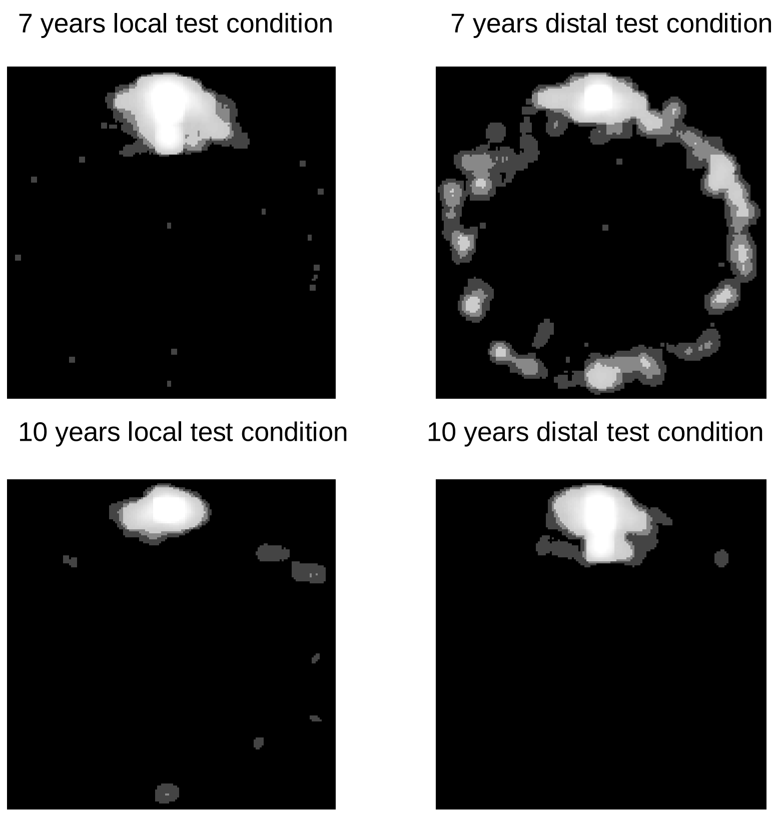

Figure 4. Density plot of the response locations for both age groups per test condition. The plots are normalised so that the correct location is at the top. The 7-year-olds in the *distal* condition showed a different pattern of response locations (upper right) compared to the other groups.

CHAPTER 7

THE ROLE OF LANDMARKS AND BOUNDARIES IN THE DEVELOPMENT OF SPATIAL MEMORY

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. The role of landmarks and boundaries in the development of spatial memory (*in press).* Developmental Science

Abstract

It has been suggested that learning an object's location relative to (1) intramaze landmarks and (2) local boundaries is supported by parallel striatal and hippocampal systems both of which rely upon input from a third system for orientation. However, little is known about the developmental trajectories of these systems' contributions to spatial learning. The present study tested 5 and 7-year-old children and adults on a water maze-like task in which all three types of cue were available. Participants had to remember the location of an object hidden in a circular bounded environment containing a moveable intramaze landmark and surrounded by distal cues. Children performed less accurately than adults, and showed a different pattern of error. While adults relied most on the stable cue provided by the boundary, children relied on both landmark and boundary cues similarly, suggesting a developmental increase in the weighting given to boundary cues. Further, adults were most accurate in coding angular information (dependent on distal cues) whereas children were most accurate in coding distance, suggesting a developing ability to use distal cues to orient. These results indicate that children as young as 5 years use boundary, intramaze landmark, and distal visual cues in parallel, but that the basic accuracy and relative weighting of these cues changes during subsequent development.

7.1 Introduction

As we find our way during everyday tasks, our spatial navigation is guided by an interaction between perceived environmental information and memories of where things are and how we got to them in the past. Different categories of learning processes have been proposed to support mammalian navigation, with differential dependencies on different neural systems. A distinction is made between *place* learning and *response* learning (Packard & McGaugh, 1992, 1996; Tolman et al., 1946; White & McDonald, 2002) or equivalently between *locale* and *taxon* navigation (O'Keefe & Nadel, 1978). *Place* or *locale* refers to knowledge of a location defined in terms of distance and direction to the configuration of surrounding environmental information, which can consist of landmarks and/or the geometry of the environment. The location of the self or of an object can be resolved flexibly, e.g. as when starting from a new position, and relies heavily on the hippocampal system (Cohen & Eichenbaum, 1993; Hartley et al., 2003; Iaria et al., 2003; O'Keefe & Nadel, 1978; Packard & McGaugh, 1996). By contrast, *response* or *taxon* refers to behaviour which is directly guided by sensory information (as when the target location is visible, or at the end of a marked path) or which inflexibly re-instantiates a previous sequence of movements, and relies on the striatal system (e.g. Hartley et al., 2003; Iaria et al., 2003; Packard & McGaugh, 1996).

Spatial tasks originally developed to study *place* and *response* learning systems (or *locale* and *taxon* navigation) in rodents were the cross maze paradigm (Tolman et al., 1946), and the Morris water maze (Morris, 1981). The latter task has been widely used to specifically study *place* learning (e.g. Hamilton et al, 2007; 2008; Maurer & Derivaz, 2000; Morris, 1982; Pearce et al., 1998). The Morris water maze consists of a large circular pool in which rats are required to escape from the water by swimming to a platform hidden just under the surface. It has been shown that learning of the platform location depends on the hippocampus (Morris et al., 1982). The animal remains oriented by the distal cues hung around the pool, while the response location is defined relative to the boundary of the pool (Hamilton et al, 2007; 2008; Maurer & Derivaz, 2000). By contrast, learning to locate a platform whose location is paired with an intra-maze landmark (both are moved together within the pool between trials) is not hippocampal dependent (Pearce et al., 1998).

Orientation relative to distal cues is most likely maintained by the system of 'head-direction cells' found along Papez's circuit (Taube, 1998) which projects into both the hippocampal formation and the striatum, consistent with the performance deficits on this task after anterior thalamic lesions (Wilton et al., 2001). Location relative to environmental boundaries is most likely maintained by the 'place cells' found in the hippocampus (O'Keefe, 1976), which respond in locations defined by environmental boundaries (O'Keefe & Burgess, 1996) rather than intramaze landmarks (Cressant et al., 1997).

Following these studies, Doeller and Burgess (2008) investigated the role of boundaries and landmarks, and their related neural structures (Doeller et al., 2008), in human spatial learning. They dissociated participants' ability to learn locations relative to a local boundary (boundary-related learning) and to a local landmark (landmark-related learning) within a single virtual reality (VR) task (Doeller and Burgess, 2008), which was also included in a fMRI study (Doeller et al., 2008). The VR environment comprised a circular-bounded arena, containing an intramaze landmark and surrounded by distal landmarks. The distal landmarks provided information about the participant's orientation. Participants saw the locations of different objects hidden around the virtual arena. They were then moved to a different location and facing direction within the arena and asked to navigate to each hidden object's place. Representing locations either relative to (i) the boundary of the arena and distal landmarks, or (ii) the internal landmark and distal landmarks, would suffice to relocate the objects. To separate these two kinds of coding, the internal landmark and the boundary were moved relative to each other between test blocks. Unbeknownst to participants, some of the hidden objects were associated with the landmark, and thus moved with it between test blocks (keeping a fixed distance and direction relative to the landmark), while other objects were associated with the boundary, and so kept a fixed distance and direction relative to the boundary. This study was thus able to determine the extent to which the participants relied on either cue (when movement of the landmark brought them into conflict), and the extent to which they learnt over the course of the study that the boundary was reliable for finding one subset of objects, whereas the landmark was reliable for finding the other.

Note that in this paradigm, both types of learning depend on also orienting correctly with respect to the distal landmarks. Thus as the object is not directly placed at the internal landmark, the correct angle from it also needs to be known. Therefore, simple "*response* learning" is not sufficient to relocate any of the objects given the participant's new starting locations on each trial. The results demonstrated that navigation based on the boundary and distal orienting cues was distinguished from navigation based on the local landmark and distal orienting cues by operating via different learning rules (Doeller and Burgess, 2008), and, as shown in the fMRI experiment, by producing differential activation of the hippocampal and striatal systems (Doeller et al., 2008). Furthermore, it was shown that the learning systems do not compete (cf. Poldrack et al., 2001), but that they independently influence behavior at similar rates, and act in parallel during learning. In the present study we adapted this task with the aim of examining the developmental trajectories of these two systems in children.

Given that studies using (adaptations of) the Morris water maze provided evidence for specific brain-behavior relationships in animals (Pearce et al., 1998) and adult humans (Doeller et al., 2008), when tested on the same task, inferences might be made about the ontogeny of the neural systems involved in learning behavior in children (Overman et al., 1996a). That is, children's ability to learn locations relative to environmental boundaries and intra-maze landmarks might provide some insight into the relative developmental time-courses for the functional maturation of the hippocampal and striatal systems involved in human wayfinding. Similarly, previous developmental studies, which used paradigms related to the Morris water maze to study (local and distal) landmark use in children at primary school age, showed that *place* learning and *response* learning can be dissociated in terms of their developmental trajectories, with spontaneous *response* learning being present early in life (at least at the age of 5 years) and *place* learning developing up until the age of 7 to 10 years (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003; Overman et al., 1996b) which can possibly be related to a late maturation of the hippocampus (Newcombe & Huttenlocher, 2000; Overman et al., 1996b). However, accurate representations of locations within the testing room also appear to be present at younger ages (Nardini et al., 2006).

The present study aimed to provide a parametric measure of accuracy for boundary-related and landmark-related learning, so that their interaction and development could be studied. To do this we adapted the paradigm of Doeller and colleagues (2008) testing children and adults' recall for locations in a (real life) circular environment containing an experimentally controlled landmark and surrounded by distal orientation cues. The design was the same in that the landmark moved relative to the boundary between test blocks so that landmark and boundary cues were placed in conflict. Participants had to learn the location of two objects, of which one was associated with the landmark and the other with the boundary.

7.2 Method

7.2.1. Participants

Twenty-nine children and sixteen adult students participated in the study which was conducted at the Visual Development Unit at Oxford University. The children comprised two age groups: 5-year-olds (n = 13, number of girls = 6; mean age = 5.5, *SD* = 0.16 years) and 7-year-olds (n = 13, number of girls = 8; mean age = 7.4, *SD* = 0.32 years). Three additional children were excluded from analysis because of interruptions in the testing which could have interfered with learning. All children came from a database of volunteers recruited in Oxford, and parents gave consent for their child's participation in the study. Adult students (mean age = 20.0, *SD* = 1.70 years) were recruited through advertisements at Oxford University. They received course credit or payment for participation and gave written consent. All children and adults reported to be healthy, had normal or corrected to normal vision and were unaware of the rationale of the study.

7.2.2. Apparatus and Stimuli

The circular arena in which the children and adults were tested was formed by an empty circular swimming pool with diameter 366cm and walls of height 91cm (see Figure 1). This pool was placed in a rectangular testing room (4.9m x 6.7m) whose walls were covered with black ceiling-to-floor curtains. The testing room was dark except for a projection light placed directly above the center of the pool. Owing to the black curtains and low light, the shape of the surrounding room was not discernible, so it was not possible to use the geometry of the room as a cue. The floor of the pool was covered with blue linoleum in which eighty-eight 32cm x 32cm 'doors' (hiding locations) were cut. Participants searched for laminated 21.5cm x 21.5cm pictures of a frog and a ladybird, which could be hidden under different 'doors' in the floor. Due to the material used, the cuts of the doors were not visible; therefore participants could not use a counting strategy to code location. The landmark inside the pool consisted of a traffic cone (height 70cm, diameter 25cm), which was round with no cues to its orientation. The distance between the landmark-related object and the landmark was 86cm. The more distant cues surrounding the arena were LED arrays measuring 30cm x 15cm which formed an array of a "moon", a "lightning bolt" and a "star", and were placed at distance 110cm and heights 1.60m, 1.83m and 1.63m respectively on one side of the room, and an array of mountains cut from cardboard paper (168cm x 69.4cm) placed at distance 110cm and height 110cm on the other side of the room.

The distal cues, which were deliberately made very different and distinctive to aid orientation, were similar in total width and were located at an absolute distance of 2.93m from the centre of the pool. A light, not visible from inside the pool, was projected at the mountains.

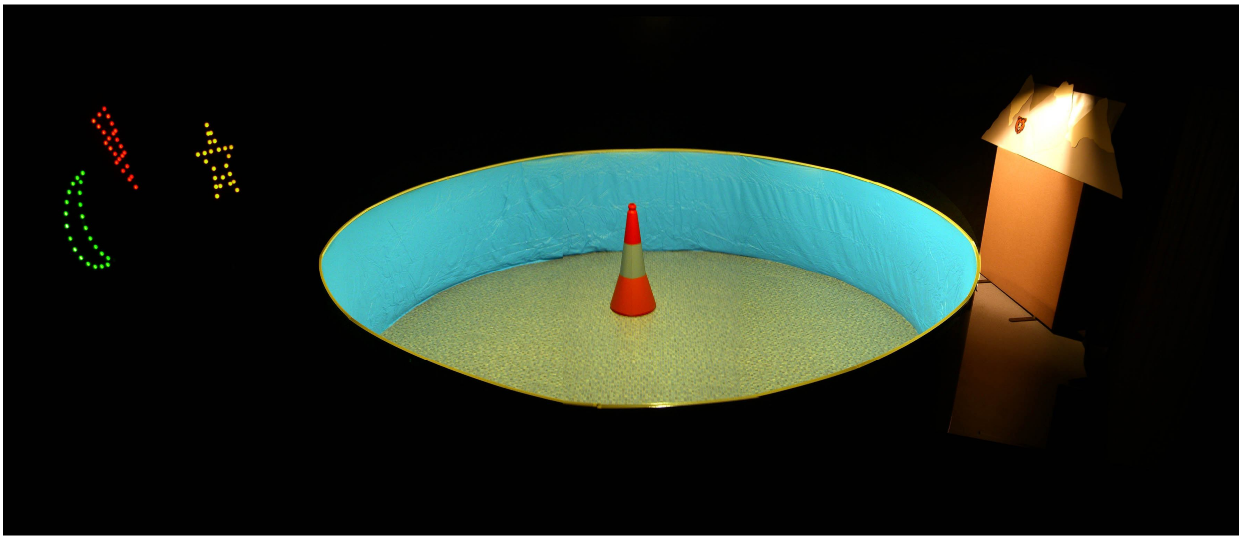

Figure 1. Experimental set-up showing the circular arena with the intramaze landmark (traffic cone), the boundary (circular wall of the pool) and the extramaze orientation cues (three differently lights and the mountains cut from cardboard paper).

7.2.3. Design

Participants had to remember the locations of two objects (frog and ladybird pictures) of which one remained at a location fixed relative to the boundary of the pool, while the other remained at a location fixed relative to the intramaze landmark (traffic cone). That is, between test blocks the landmark and the boundary were moved relative to each other, and the landmark-related object moved with the landmark between test blocks (keeping a fixed distance and direction relative to the landmark), while the boundary-related object kept a fixed distance and direction relative to the boundary, see Figure 2a. At the beginning of the experiment, each object was shown in its correct position, which was the same for all participants; starting with the landmark in the upper right corner and the two objects at equal distance from the landmark and the boundary. These distances were equal in the first block so that there was initially no reason to associate either object more strongly with either cue, Figure 2a. For the second and third test blocks, the landmark and landmark-related object were moved to a predefined location in quasi random order, Figure 2b. The assignment of either object location as boundary-related or landmark-related, as well as the assignment of the 'frog' or 'ladybird' as a boundary or landmark-related object, and the order of movement of the intramaze landmark (traffic cone) was randomized between participants. The relationship between the possible locations for the boundary-related object and the distal cues (lights and mountains) can be seen in Figure 2a. The experiment comprised three test blocks of four trials, in which each trial consisted of the retrieval of both the boundary and landmark-related objects, thus twenty-four responses in total.

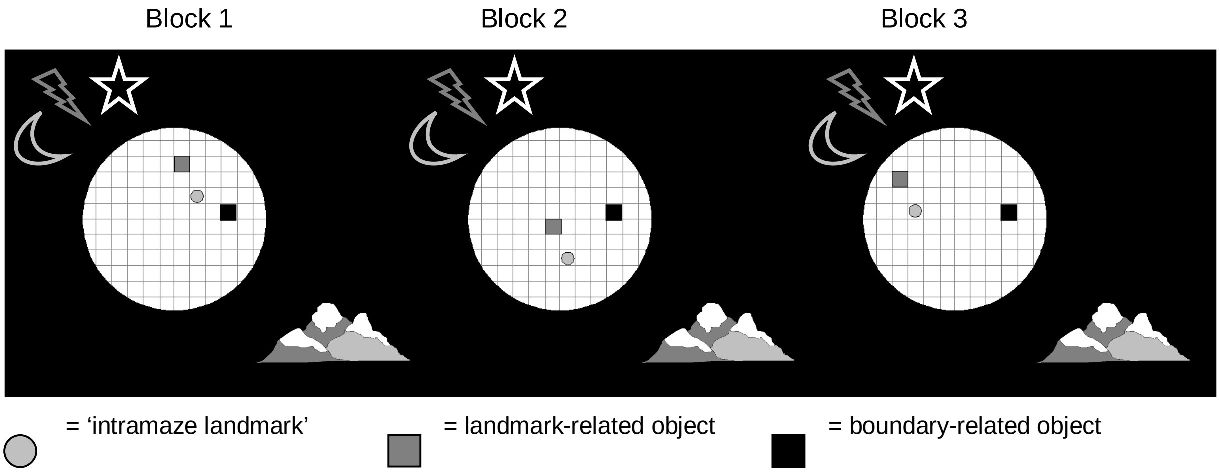

Figure 2a. Experimental Design: Participants learned two object locations over three blocks with the landmark (light grey circle) and the boundary moving relative to each other at the start of each block. One of the objects was associated with the landmark (dark grey square) and the other object was associated with the boundary (black square). The distal cues are presented as how they were actually positioned during the experiment.

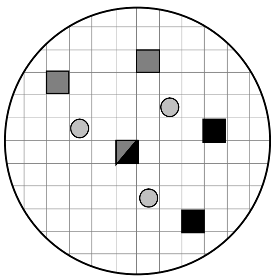

Figure 2b. Experimental Design: Locations of the landmark (light grey circle) and the possible locations of the landmark related and the boundary-related objects (dark grey and black squares). The assignment of either object location as boundary-related or landmark-related, as well as the assignment of the ‘frog’ or ‘ladybird’ as boundary-related or landmark-related was randomized between subjects. All participants started the experiment with the landmark in the upper right corner and the two objects at equal distance from the landmark and boundary, as shown in Figure 2a (Block 1).

7.2.4. Procedure

Participant and experimenter entered the arena using the pool ladder, which was then removed out of sight. Participants were encouraged to take a good look around and to name everything they saw. The experimenter made sure that the intramaze landmark (traffic cone) as well as each of the distal cues was pointed out. Next, participants were told that the experimenter had a ‘secret’, namely that two pictures were hidden underneath the carpet in the pool. Then the locations of both pictures were shown to participants who were told to remember both locations very well, since they would be asked to find them again. After that, participants were taken to the center of the pool and asked to close their eyes. To disorient participants (so that they had to use visual cues to find the pictures), they were first rotated several times while the experimenter moved around in different directions in order not to provide a directional cue herself. Then, the participants were taken along a wandering path, still with eyes closed, to one of four positions on the north, east, south or west side of the pool, facing the pool wall. After participants had reached this starting point, they were asked to count to twenty out loud still with eyes closed. During this period the experimenter, if necessary (i.e. on the first trial of a new test block), covertly moved the landmark and the picture related to it to their new position. Subsequently, participants were asked to open their eyes and turn around. They were provided with a copy of one of the hidden pictures and told to place it on top of the carpet where they thought the original picture was located. Then feedback was provided: The experimenter showed participants the correct location of the hidden picture. This procedure was repeated for the second picture. The order in which the two pictures were retrieved varied randomly from trial to trial. Then the participant proceeded to the next trial, starting with the disorientation procedure in the center of the pool. Throughout testing, the experimenter stayed in the pool with the child, but moved around in order to avoid becoming a stable landmark herself.

7.3 Results

Here we will discuss participants' overall performance on the task, the extent to which their errors can be explained by reliance on the incorrect cue and how participants had used the landmark and/or boundary in order to locate the objects, thereby differentiating between distance and angular scores.

7.3.1. Overall performance

The first analysis focused on participants' overall accuracy at relocating the objects. Performance was calculated based on the distance (error) between a subject's response and the target object's true location. Since the raw distance (cm) does not give an equivalent measure of performance for objects near the edge and those near the centre of the arena (with the latter ones, on average, getting smaller errors if responding was at chance, i.e. uniformly randomly distributed in the pool), we transformed raw distance to a standardized performance score. This score is equivalent across locations in that it is scaled against the level of performance that would be expected by chance. Distances were transformed into standardized performance scores with the formula: performance score = 100 x (chance distance – error distance) / chance distance (see Nardini et al., 2006). Chance distance was calculated as the average of the distances from each of the 88 possible response locations to the correct location. Following this transformation, a score of 0 indicates chance performance, while a score of 100 indicates a correct search. A score below 0 indicates an error greater than that expected by chance.

Figure 3a plots performance by age group, object type, and block (1-3), for each block's four individual trials (left) and collapsed over the whole block (right). The two child groups made large errors, but tended to attain above-chance performance throughout. Adults' performance was close to ceiling, with the exception of the landmark-related object on the first trials of blocks 2 and 3; these were the trials immediately after the landmark and landmark-related object had moved relative to the boundary.

These standardized performance scores were subjected to a repeated measure ANOVA with Group (1-3) as between-subjects factor and Type of Object (landmark-related or boundary-related), Block (1-3) and Trial (1-4) as the within-subjects factors. The analysis revealed a significant effect of age group (F (2,39) = 103.86, p < .0001). Despite the fact that all age groups significantly performed above chance level on the task: 5-year-olds, t (12) = 6.71, p < .0001; 7-year-olds, t (12) = 5.67, p < .0001 and adults, t (15) = 66.48, p < .0001, post hoc comparisons (Bonferonni corrected) showed that both child groups (5-year-olds = 22.7% and 7-year-olds = 29.1%) differed markedly from the adults (83.7%) on overall performance score (p's < .0001), however, the child groups did not differ significantly from each other (p = .31). Additionally, the children differed markedly from the adults on most (or a combination) of the above mentioned factors; Group x Type of Object, F (2,39) = 5.12, p < .05; Group x Trial, F (6,117) = 4.81, p < .0001; Group x Block x Type of Object, F (4,78) = 2.88, p < .05; Group x Type of Object x Trial, F (6,117) = 5.41, p < .0001; Group x Type of Object x Block x Trial, F (12,234) = 2.37, p < .01. Most importantly, post hoc paired-samples T tests (alpha adjusted) showed that, for the second and the third test block the adults performed significantly better on the boundary-related object than on the landmark-related object, t (15) = -6.74, p < .0001. The 5 -and 7-year-olds, on the other hand, showed no difference in performance on the two object types: 5-year-olds, t (12) = -1.75, p = .11 and 7-year-olds, t (12) = .63, p = .54. The result that adults performed worse on the landmark-related object suggests that they relied more on the boundary than on the intramaze landmark. By contrast there was no such significant difference in the child groups.

7.3.2. Performance relative to the incorrect cue

To check the extent to which errors were explained by reliance on the “wrong” cue for a given object, standardized performance scores (standardized in the same way as described for the overall performance scores), which again consisted of distance errors, were calculated relative to the search place predicted by the landmark (for the boundary object) and by the boundary (for the landmark object). This analysis was carried out for blocks 2 and 3 (since in block 1, both cues predicted the same locations). Figure 3b plots these scores. While there seems to be no strong indication of the child groups searching with respect to the wrong cue, it is clear that adults’ large errors in locating the landmark-related object after the landmark and object moved (Figure 3a) are explained by searches close to the place predicted by the boundary (Figure 3b), i.e. the object’s location within the arena before it and the landmark moved.

These scores relative to the location predicted by the use of the incorrect cue were subjected to a repeated measure ANOVA with Group (1-3) as between-subjects factor and Type of Object (landmark-related or boundary-related), Block (1-2) and Trial (1-4) as the within-subjects factors. The analysis did not show a main effect for Group, F (2,39) = 1.47, p > .05. However, the factor Group did interact with the other factors; Group x Type of Object, F (2,39) = 6.58, p < .01; Group x Block, F (2,39) = 4.10, p < .05; Group x Trial, F (6,117) = 6.72, p < .0001, and there was also a three-way interaction of Group x Type of Object x Trial, F (6,117) = 7.94, p < .0001. This latter interaction showed that when the configuration of the maze changed, the adult, but not child participants, tended to relocate both objects relative to the boundary thereby ignoring the landmark.

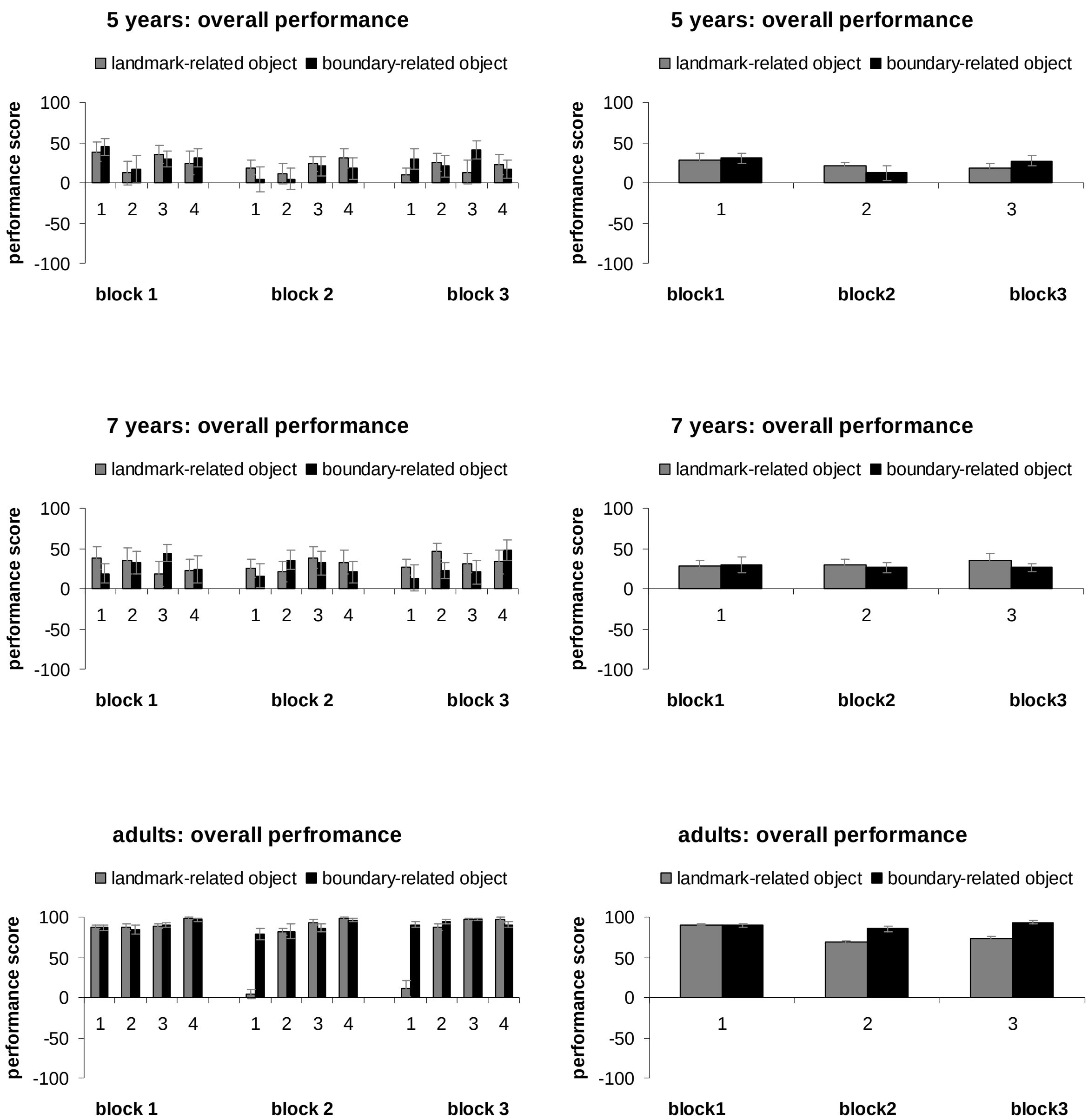

Figure 3a. Standardized performance scores based on distance of the response location to the correct location for all three age groups, shown by block and object type for the four trials in each block (left) and collapsed by block (right).

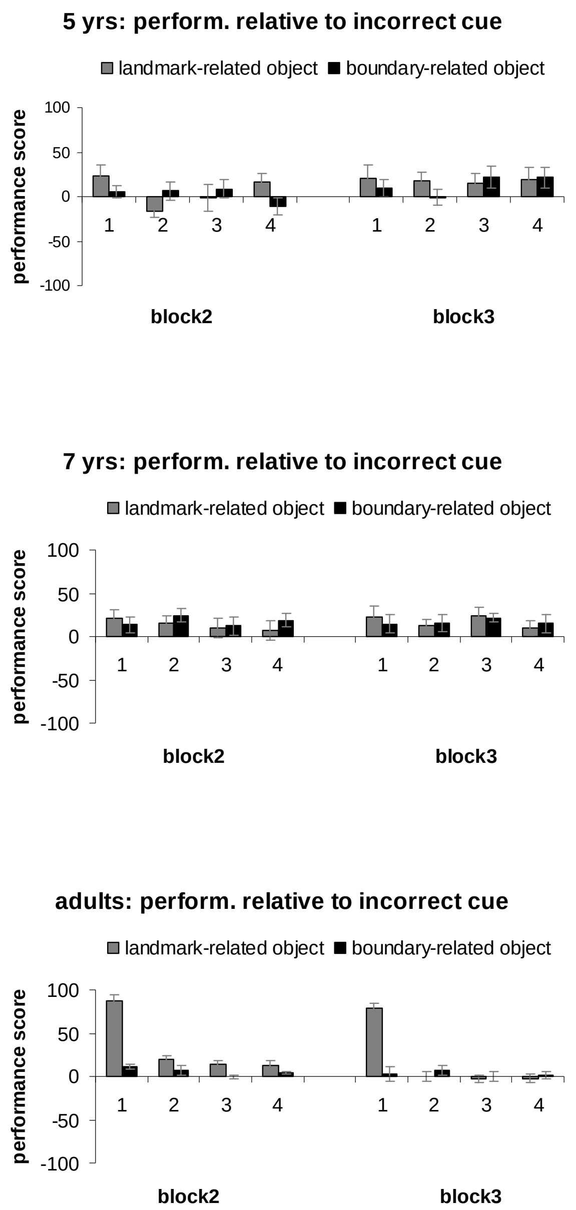

Figure 3b. Standardized performance scores based on distance of the response location to the location predicted by the use of the incorrect cue for all three age groups, shown by block and object type for the four trials in each of blocks 2 and 3.

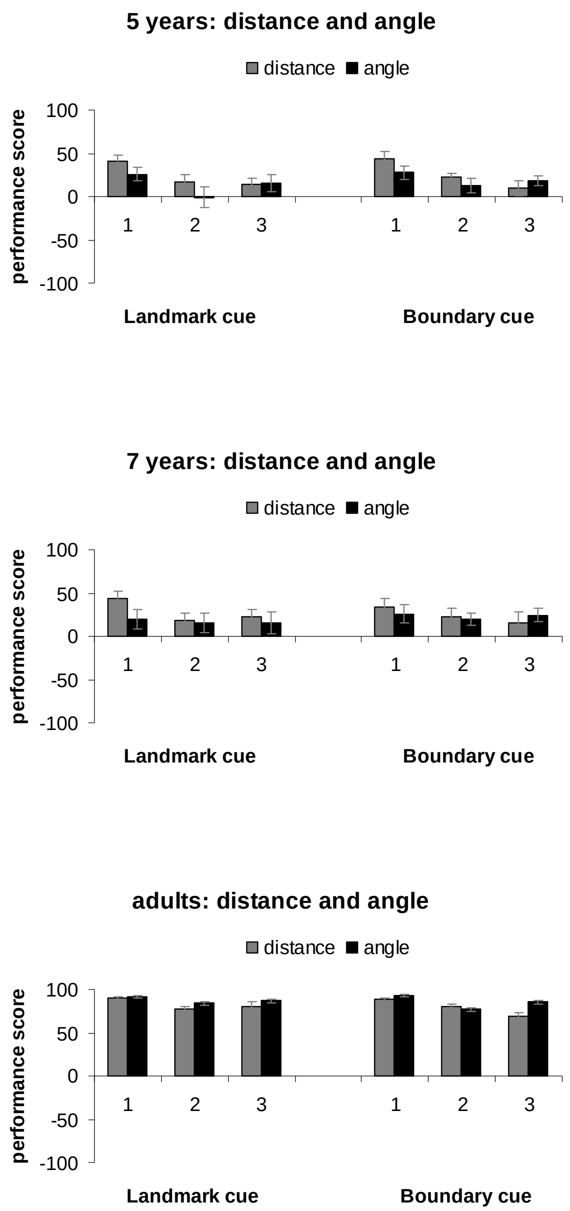

Figure 4. Standardised scores for distance and angular performance relative to the landmark and boundary, shown for both objects combined, across the three blocks, see Figure 5.

7.3.3. Cue use: distance and angle

To gain more insight into how participants used the landmark and/or boundary cues in localizing the objects, distance and angular accuracy was examined separately relative to both cues. To calculate a distance performance score, the distance between a participant's response and the boundary or landmark was compared with the correct distance between the hidden object and the boundary or landmark, scaled against the discrepancy between these that would be expected by chance (as before) – see Figure 5. To calculate an angular performance score, the angle of a response from the boundary or landmark was compared with the actual angle of the hidden object from the boundary or landmark, scaled against the discrepancy between these that would be expected by chance; see Figure 5. Note that this measure does *not* reflect the relative influence of either cue on the participant's response. When an error occurs, e.g. responding in the location predicted by the boundary for a landmark-related object, these four measures separately reveal the extent to which the incorrect location nonetheless maintains the correct angle or distance to landmark or boundary.

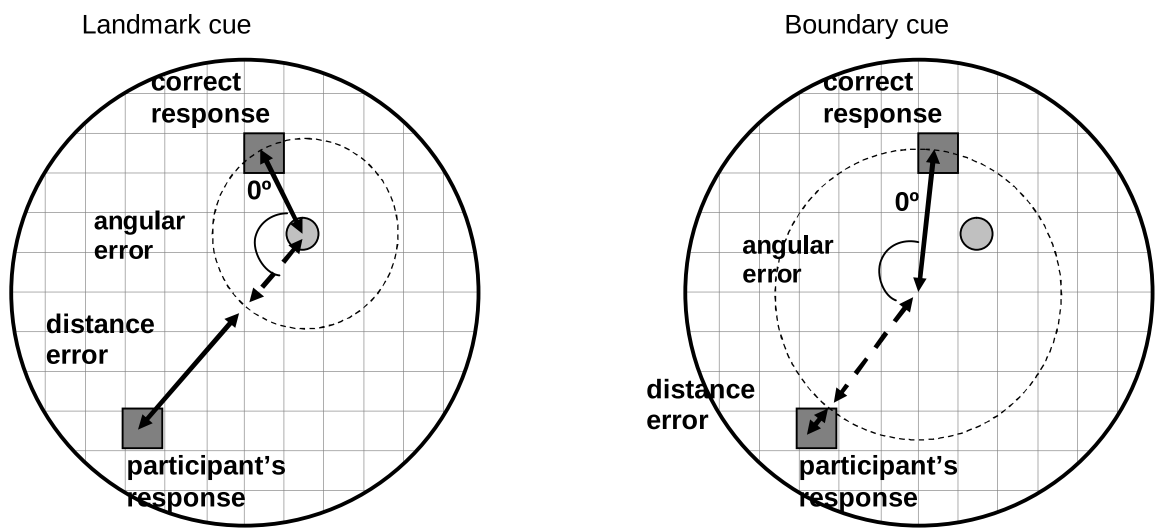

Figure 5. Measures of distance error and angular error relative to the landmark and boundary cues. To calculate the distance performance score, the distance between a participant's response and the boundary or landmark was compared with the correct distance between the hidden object and the boundary or landmark, scaled against the discrepancy between these that would be expected by chance. Likewise, to calculate the angular performance score, the angle between a participant's response and the boundary or landmark was compared with the correct angle between the hidden object and the boundary or landmark. These distance and angular performance scores were converted to standardized scores by taking into account the differences between correct and measured distances and angles that would be expected by chance.

Figure 4 plots these standardised distance and angle performance scores by age, block and object type. These scores were subjected to a repeated measure ANOVA with Group (1-3) as between-subjects factor and Block (1-3), Cue Type (landmark or boundary) and Measure (distance or angle) as the within-subject factors. The most important finding from this analysis was a two-way interaction between Measure and Group, F (2, 39) = 5.70 p < .05, which indicated that the relative amount of error in angle vs. distance changed with age. A post hoc analysis with adjusted alpha found that overall the children performed significantly better on the distance measure than the angular measure (t (25) = 2.42, p < .05) whereas the adults performed significantly better on the angular measure in comparison with the distance measure (t (15) = -5.71, p < .0001). No effects were found for the factor Cue Type (*p's* > 0.05).

7.4 Discussion

In the present study, children aged 5 and 7 years and adult students were tested in a real life object location memory task in which they were required to find two hidden objects. One of the objects was related to an intramaze landmark which moved between test blocks and the other object was related to the circular boundary of the environment. Both landmark and boundary cues were useful only in conjunction with the orientation provided by the stable distal landmarks surrounding the maze. Participants' performance on either object type indicated their ability to code the object's location relative to either the intramaze landmark or the boundary of the environment.

Overall, although adults performed markedly better than children, all age groups were significantly above chance (Figure 3a). However, adults tended to be less successful at finding the landmark-related object than the boundary-related object – they relied more on the boundary than on the landmark, and so searched incorrectly after the landmark and landmark-related object moved. These incorrect searches were close to the place predicted by the boundary (Figure 3b). There was no significant difference in children's performance with the two object types. This suggests that children's weighting of boundary vs. landmark information was different to adults'; they did not rely so strongly on the boundary, but seemed to rely similarly weakly on both cues. This is consistent with other suggestions that the weighting of spatial cues changes in development (Newcombe & Hutttenlocher, 2006; Learmonth et al., 2008).

Differential weighting could be adaptive if it reflected developmental changes in the underlying reliabilities of the different information sources (Cheng et al., 2007). Thus if development in the accuracy of using two kinds of spatial information sources were uneven, it could be adaptive to weight one source more at an early age, and the other source more at a later age. The present results could therefore correspond to an adaptive reweighting (see also Newcombe & Ratliff, 2007). Alternatively, children's apparently even weighting in the present study, compared with adults' uneven weighting could indicate a failure to integrate the different sources of information at all (see Nardini et al., 2008). To settle this question, future research should isolate boundary and landmark cues to determine developmental changes in their accuracy individually, and manipulate the reliability of each cue for finding the target. Reliability can be manipulated by varying the proximity of the hidden object to the landmark or boundary, or by varying the size of the landmark and/or the height of the boundary. In addition, the configuration of boundaries and/or landmarks can be manipulated to reveal their influence on responding (e.g. Hartley et al., 2004; Maurer & Derivaz, 2000; Nardini et al., 2006). One issue to consider is the potential effect of the different heights of the children and adults. We note that all children were taller than the pool wall so that their view on the distal landmarks was not obscured, and that both types of cue (landmark and boundary) would appear taller to the children than to the adults. Nonetheless, it is still possible that the extra relative height of the pool wall for the children might have contributed to their diminished use of the distal landmarks, or have otherwise affected the salience or apparent reliability of the different information sources (see also Newcombe & Ratliff, 2007), and thus affected their relative influence (Nardini et al., 2008).

The fact that the adults seemed to have focused solely on the boundary and distal cues for orientation, thereby neglecting the intramaze landmark has some echoes in the animal literature. When the location of a food reward was paired with distinct landmarks, rats ignored the landmarks when their locations were varied relative to the background, whereas they used the combination of landmarks and background when they remained fixed relative to each other (Biegler & Morris, 1993). Nonetheless, the study by Pearce et al. (1998), using the Morris water maze paradigm, demonstrated that rats can associate a goal location with an intra-maze landmark that moves relative to the background cues. A similar result was found in the VR study (Doeller et al., 2008) in which adults showed a similarly strong influence of both cues. Our finding that adults neglect the intramaze landmark might be taken as a sign that, although it has been previously shown that testing in virtual and real environments lead to similar results (Péruch & Wilson, 2004), in our experiment, adults experienced the real boundary and distal cues as relatively more stable than in the VR environment. This might relate to the process of walking through the surrounding building before starting the experiment, or the fact that the distal orientation cues provided motion parallax indicating that the boundary was fixed, while in the VR experiment, the distal cues were rendered at infinity and so did not contribute to judgements of the location of either boundary or landmark. In line with the suggestion to systematically vary the salience of the cues to investigate its effects on developmental patterns in the differential weighting of cues, future studies could attempt to strengthen the association of the object location to the landmark by hiding the object closer to it, or by increasing the size of the landmark, as both manipulations were found to increase the influence of the landmark on response location in the VR studies.

Although the performance of the children was much worse than that of the adults, it was better than chance, indicating an ability to use the distal orientation cues in addition to the landmark or boundary. Previous studies have indicated that when distal and proximal landmarks conflict, children do not select the distal landmarks until school age (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003). However, when there is no conflict, children as young as 3 years can use distal natural landmarks to reorient (Smith et al, 2008), and may rely on them preferentially when in conflict with unstable local landmarks (Nardini et al., 2006). In the present study, children's above-chance scores on the main measure and on the angular measure indicate that they did use the distal cues to some degree to determine orientation. This finding is consistent with the extensive literature on children's ability to reorient in an enclosed environment, which shows that, when tested in a large enough testing room (8 by 12 feet) children aged 18 months are already able to, in combination with geometric information provided by the room, use landmark information to reorient (Learmonth et al., 2001; Cheng & Newcombe, 2005). Interestingly, 3 to 6 year-olds' use of landmark information depends on ease of movement and distance of the landmark (distant landmarks being used more reliably) (Learmonth et al., 2008). In the present study, children were able to freely move around in the pool, and the distance of the distal cues to the centre of the search space was larger (2.93m vs. 1.83m) than in reorientation studies using the 8 by 12 feet room. Both these factors would be expected to facilitate landmark use.

In addition to the above described results, an overall difference between adults and children was found in the way they used distance and angular information to relocate both object types. Children were more accurate on distance, whereas adults were better on angle than on distance. Since judging angle required the use of the distal cues, this indicates that the developmental change was in better use of the distal cues for orientation. Thus, although children 5 and 7-year-olds seem to have used some combination of distance and angle information (the latter dependent on distal cues), they did not yet combine these to attain adult-like accuracy. They also relied relatively more on coding distance to the landmark and boundary cues. We might speculate that children's difficulties in using distal cues for orientation relate to their difficulties in using category information along the dimension of angle (Huttenlocher et al., 1994; Sandberg & Huttenlocher, 1996).

Relating back to the neural correlates associated with boundary-and landmark-related learning, as discussed in the introduction, the above chance performance of all age groups is consistent with evidence that, in rats, the hippocampus is functionally mature very early in life (Martin & Berthoz, 2002), and 18 month-old to 3-year-old children are able to locate objects relative to the experimental room (Nardini et al., 2006; Newcombe & Huttenlocher, 2000). The absence of a bias towards use of the boundary in the 5-year-old children tested here might also indicate that striatal dependent representations (i.e. response learning or landmark-related learning) are equally mature at this age (Overman et al., 1996a; Overman et al., 1996b). However, the low overall level of performance in these children rules out firm conclusions regarding the relative development of these two systems, and the finding that the children erred more in the direction of the responses than in the distance from the two types of cue may simply indicate poor use of the distal orientation cues. It is possible that the process of disorientation between trials was more disruptive for children than adults. Thus the adults may have been better at reorienting themselves relative to the distal cues at the start of each trial, possibly reflecting the developmentally delayed influence of distal cues in conflict situations referred to above. The orientation of the place cell representations in rats becomes decoupled from distal cues when the rat is disoriented before each trial (Knierim et al., 1995) or when the distal cues appear to be unstable relative to the rats internal sense of direction (Rotenberg & Muller, 1997; Jeffery & O'Keefe, 1999). As mentioned earlier in the discussion, inability to combine different sources of information (in this case conflicting path integrative and visual cues) up to 8 years have been recently reported in both spatial (Nardini et al., 2008) and non-spatial situations (Gori et al., 2008).

In conclusion, we found evidence for differential object location learning patterns in children aged 5 to 7 years and adults. While orienting in a maze, children seem to have used both landmark and boundary cues in order to relocate different object types, and were relatively more accurate in coding the distances than angles to these cues. Adults on the other hand relied more on the stable environmental cues, and were more accurate in coding angular information provided by distal (extramaze) landmarks than distance information. In addition to the 5 and 7-year-old children tested here, future studies may test older children to address the point in development at which the adult pattern of behaviour emerges. That is, in line with place learning continuing to develop well into the school years (Lehnung et al., 1998; Lehnung et al., 2003; Leplow et al., 2003; Newcombe et al., 2007), it would be interesting provide a more thorough evaluation of the developmental trajectory for landmark and boundary-related learning. Furthermore, future research should systematically vary the salience of the cues to investigate its effects on developmental patterns in the differential weighting of cues, and determine in more detail how the ability to combine angular and distance information for boundary and landmark cues develops. Lastly, developmental imaging studies using virtual reality could provide insight into the maturation of specific neural structures associated with the different types of learning.

CHAPTER 8

GENERAL DISCUSSION

General Discussion

8.1 Summary

Knowledge of how spatial cognition develops is central to our understanding of cognition in general (Newcombe & Huttenlocher, 2000). In this thesis, we tried to obtain more insight in the question how children learn to deal with space. We conducted several developmental studies on spatial memory that relate to this question, and which are presented in the chapters of this thesis. We first studied children's ability to code visuo-spatial information, i.e. spatial relations within objects (chapter 2). We were interested in how children code categorical and coordinate spatial relations within an object, whether this develops with age, and if so whether corresponding changes in hemispheric specialization can be observed. In the following chapters, we investigated children's (and adults') ability to represent visuo-spatial relations in combination with other spatial information sources (i.e. movement information) in different frames of reference. Also, we examined the developmental pattern of different types of spatial coding which can be dissociated based on these reference frames. In chapter 3, we studied children's reference frame use in an object location memory task in which, on some trials, the viewpoint on a scene with objects was changed between presentation and test. In addition, we tested children's ability to reproduce categorical and coordinate spatial relations after a similar viewpoint change. We extended this study by investigating children's combined use of different types of spatial information (i.e. self-motion cues and local and distal color cues for orientation) to locate objects in the environment (chapter 4). Subsequently, we investigated children's reference frame use in a virtual reality navigation task. We were specifically interested in how the spontaneous usage of different navigation strategies develops with age and changes throughout the learning process (chapter 5). In chapter 6, we examined the extent to which the development of different types of spatial coding, dissociated based on the use of different reference frames, depend on an increment of relevant experience. At last, in the study presented in chapter 7, we investigated children's ability to learn an object's location relative to a landmark or relative to a boundary.

8.2 Development of spatial relations

In the introduction of this thesis we discussed the hierarchical dual coding model put forward by Huttenlocher and colleagues (1991). This model states that coordinate spatial information is weighted with general categorical information in order to effectively remember an object's location. In order to get a better understanding of its developmental origins, two developmental studies were conducted: one in a one-dimensional space (i.e. rectangular sandbox) (Huttenlocher et al., 1994), and the other in a two-dimensional space (i.e. pencil-and-paper circle task) (Sandberg et al., 1996). In both studies a developmental pattern was observed. The first study showed that the processing of both categorical and coordinate relations is present early in life, however, the subdivision of single-dimensional space into categories systematically improves with age. In the second study it was demonstrated that the construction of spatial categories along the dimension of both radial distance and angle only emerges between the age of 7 and 9 years, possibly due to the better processing capabilities of older children (Sandberg, 1999). Thus, young children can combine categorical and coordinate spatial relations for memorizing an object's location, however, the weight with which they are coded develops with age. In this thesis we tested whether categorical and coordinate information would be weighted differently in case of the viewpoint on a scene of objects changes (chapter 3). That is, one might expect that the certainty with which coordinate relations are encoded varies with the angle over which a viewpoint change takes place, while this angular effect might be smaller for the encoding of categorical information. Also, this so-called 'constancy' of categorical judgments and the variation of coordinate judgments may vary for children in different age groups. It was demonstrated that, contrary to our expectations, children's (5 to 10 years) performance on the categorical and coordinate trials did not vary with the angle of viewpoint change. However, in general, performance was better on the categorical trials than on the coordinate trials, indicating that children specifically relied on the categorical spatial relations to memorize object locations. At the moment, we are conducting further experiments with adults, and preliminary results provide evidence for the existence of the 'uncertainty with viewpoint change' model which we proposed (Van der Ham et al., *in preparation*). Given this fact, and in line with the results reported by Sandberg and colleagues (1996), it might be concluded that children younger than 10 years weight categorical and coordinate information different than older children and adults (Newcombe & Huttenlocher, 2000). It has been hypothesized that this is related to younger children's limited processing capacities (Sandberg, 1999).

In addition to object location memory, the processing of spatial relations is also important for object recognition. In chapter 2 we investigated children's ability to code categorical and coordinate spatial relations within and between objects. First of all, it was shown that, overall, 10 to 12-year-olds and adults detected spatial transformations better than the 6 to 8-year-olds (Huttenlocher et al., 1994; Newcombe & Huttenlocher, 2000). However, in contrast to the studies on object location memory, the children performed very poorly on the categorical trials. We suggest that participants may have employed a coordinate strategy for these trials, since presentation time was limited, and therefore it was difficult to assign an invariant abstract (e.g. categorical) spatial label to the objects presented (Laeng, 1994; Laeng & Peters, 1995: Laeng et al., 1999). Converging evidence was found in hemisphere effects: older children (10 to 12 years) and adults made fewer 'categorical' errors in the right hemisphere, which is supposed to be specialized in processing of coordinate spatial relations (Kosslyn et al., 1989, 1992, 1995).

In all, the processing of spatial relations is important for both learning and remembering what objects look like (recognition memory) as well as for remembering where objects are located (object location memory). According to the hierarchical dual coding model categorical and coordinate spatial relations are differently weighted, with categorical relations providing prototypical information. This prototypical information useful when the amount of time over which an object's location (or the angle over which one's viewpoint changes) has to be remembered is greater (Huttenlocher et al., 1991; Postma et al., 2006). It was shown that children, when the provided time to solve the task was long enough, indeed, relied more on these categorical spatial relations to memorize object locations. On basis of both studies (chapter 2 and 3) it might be concluded that children younger than 10 years weight categorical and coordinate information different than adults (Newcombe & Huttenlocher, 2000).

8.3 Development of spatial reference frames

Besides the processing of specific spatial relations, we were interested in children's ability to represent visuo-spatial information and other spatial information sources (i.e. movement information) in different reference frames. In general, two particular frames of reference can be differentiated: one in which locations of objects are represented with respect to one's own body (egocentric), and another in which locations of objects are represented in terms of distance and direction to the configuration of landmarks and/or the geometry of an environment (allocentric). Moreover there is a third mean for memorizing the location of an object: a 'visual snapshot', in which an array of objects is stored as an 'integrated' picture. In a location memory scene recognition study (chapter 3), it was shown that, although children performed better in the condition in which both an egocentric and an allocentric reference frame could be used than in the condition in which only an allocentric frame sufficed, they did perform above chance level on both conditions. Since participant did not know in advance which condition they would receive, it was concluded that children 5 to 10 years had encoded the different reference frames in parallel. This finding is in line with the suggestion that different frames of reference operate in parallel possibly already at an early age (Nardini et al., 2006).

8.4 Egocentric reference frame

Orthogonal to the (parallel) encoding of different frames of reference, different types of spatial coding are dissociated. In the introduction we discussed the following: response learning, egocentric spatial updating, place learning and allocentric spatial updating, in which the first two require an egocentric, and the latter two an allocentric reference frame. Response learning refers to behavior that is directly guided by sensory information or which inflexibly employs a limited sequence of motor acts (Hartley et al., 2003; Iaria et al., 2003; Packard & McGaugh, 1996; Rondi-Reig et al., 2006). Previous studies have shown that response learning is present early in life, and that it is not changing much with development (Newcombe & Huttenlocher, 2000). In addition, we studied the extent to which the development of response learning and place learning depends on an increment of relevant experience (chapter 6). We were specifically interested in the extent to which children could profit from feedback for improving their performance on the place learning task. As expected, we did not find any age differences between 7 and 10-year-olds on the response learning task. However, we did so for the place learning task. A different type of response learning was presented in chapter 7. That is, in landmark-related learning as defined in chapter 7, the location of an object was associated with a landmark, and in addition distal landmarks were necessary for orientation. The landmark used in this study did not have an internal axis (other than the local landmark used in chapter 6), nor was the target object directly connected to the landmark (i.e. sharing the same location). Therefore orientation information had to be provided by the distal landmarks. We contrasted landmark-related learning with boundary-related learning in children 5 and 7 years of age, and adults. All age groups performed above chance level on both learning types, showing an ability to use the distal orientation cues in addition to the landmark or boundary. However, children differed from adults in their weighting of information sources. That is, children relied less on the boundary than adults did. Instead they relied similarly on both cues and such to a weak extent.

A different type of spatial coding that requires an egocentric frame of reference, is egocentric spatial updating, which reflects our ability to update an object's location relative to ourselves. Similar to response learning, egocentric spatial updating is thought to be present early in life. Simons and Wang (1998) developed an object location memory paradigm to study egocentric spatial updating in adults, which was later adapted to study spatial updating in children 3 to 6 years of age (Nardini et al., 2006). The main result of the adult and child studies was that participants preferred a change in view caused by their own movement over a view change caused by rotation of an array with objects, despite the fact that the same visual information was provided. This finding indeed suggests that children at a young age can update their position in an environment. Previously, Newcombe and colleagues (1998) found that 22-month-old children combine movement cues (i.e. egocentric spatial updating) with the availability of distal landmarks when walking to a different position in a room before relocating an object, thus the parallel encoding of different sources of information. In chapter 4 we extended this work by manipulating the availability of both local and distal landmarks, and at the same time changing the function of these landmarks from providing a basis for the direct coding of location (as in the study of Newcombe et al, 1998) to providing a basis for orientation (Hermer & Spelke, 1994; 1996). We will come back to the results on these manipulations in greater detail when discussing the use of an allocentric representation. However, similar to the spatial updating paradigm of Simons and Wang (1998) and the (sandbox) task of Newcombe and colleagues (1998), we manipulated children's viewpoint by asking them to walk to a different position in the room between presentation and test on half of the trials. Importantly in our study all children performed above chance level on the condition in which they had to change viewpoint, and in which no visual (local or distal) landmarks were available. This again indicates that they indeed can effectively rely on their self-movement cues.

In a straightforward sequel, we investigated how the use of egocentric spatial updating (also referred to as sequential egocentric strategy, see Rondi-Reig et al., 2006), and allocentric spatial updating develops with age and throughout a series of learning trials (chapter 5). Children 5, 7, and 10 years of age were tested on a navigation task, in which they could spontaneously employ different strategies. It was shown that children 5 years of age preferred to use an egocentric spatial updating strategy over the use of an allocentric strategy, however, when required to employ an allocentric strategy, they performed above chance. This finding suggests that, even at this young age, children can very well encode both navigation strategies in parallel, but there is a strong preference to use an egocentric strategy. For the older children, both navigation strategies were observed early in training, and the children showed bi-directional switches between strategies across the probe trials (measuring the employment of certain strategies), also suggesting parallel use different navigation strategies.

In all, the results of the studies presented in chapter 4 and 5 are in line with the proposal of Newcombe and Huttenlocher (2000). These researchers stated that the developmental pattern in the use of different spatial frames of reference (and/or spatial coding related to these reference frames) reflects changes in the likelihood to use certain types of spatial coding based on the importance (or weights) attached to different information sources, rather than it reflects a qualitative shift in reference frame usage. Thus, both egocentric and allocentric strategies are encoded in parallel already early in life, but older children prefer to use different information sources compared to younger children.

8.5 Allocentric reference frame

Two types of spatial coding that require an allocentric reference frame are place learning and allocentric spatial updating. For place learning we process the spatial relations between objects in the environment in order to locate an object. As discussed in the introduction, a widely used paradigm to study place learning is the Morris water maze (Morris, 1982). However, recently it was shown that this paradigm (with a salient pool wall) actually measured directional responding rather than navigating to a precise spatial location in space (Hamilton et al., 2007; Hamilton et al. 2008). In two chapters of this thesis, we investigated place learning (see chapter 6) and boundary-related learning (i.e. directional responding, chapter 7) in children. As described above, in chapter 6 we studied the development of response learning and place learning in a learning paradigm. In line with our expectations, we did not obtain age differences on the response learning task, however, it was shown that 7-year-old children performed significantly worse on the place learning task, than 10-year-olds. Interestingly, the youngest children improved performance after having received feedback about their performance. The fact that 'younger' children (up to 8 years) do not use distal landmarks for coding location spontaneously, might indicate that they consider these cues less important, and thus attach less weight to them (Newcombe & Huttenlocher, 2000; Newcombe & Ratliff, 2007).

We also investigated children's ability to show boundary-related learning (chapter 7). Children 5 and 7 years of age, and adults learned the association between an object's location and a local landmark (discussed above) and the association between an object's location and a boundary. Importantly, in order to correctly relocate both object types, distal landmarks were necessary for orientation. It was shown that all age groups were able to use distal orientation cues in addition to information provided by the landmark or by boundary of the enclosed environment. Thus, already at 5 years, children can combine distance (from the landmark or boundary) and direction information. This is in accordance with the extensive literature on children's ability to reorient in an enclosed environment, which shows that, when tested in a large enough (rectangular) testing room children aged 18 months are able to, in combination with geometric information provided by the room, use landmark information to reorient (Learmonth et al., 2001; Cheng & Newcombe, 2005). It was hypothesized that the results of chapter 7 could be explained by the 'adaptive weighting' of different information (Newcombe & Huttenlocher, 2000; Newcombe & Ratliff, 2007). Alternatively, children's even weighting of local landmark, boundary, and distal cues for orientation in the study presented in chapter 7 could indicate a failure to integrate the different sources of information at all (see Nardini et al., 2008). Future research should isolate boundary and landmark cues to determine developmental changes in their accuracy individually, and manipulate the reliability of each cue, in order to investigate the tenability of these accounts.

As already mentioned earlier, in chapter 4 we investigated children's combined use of different types of spatial information to locate objects in the environment. In addition to the extensive literature on children's ability to reorient in an enclosed environment (Learmonth et al., 2001; Cheng & Newcombe, 2005), we were interested in children's ability to update their spatial location (and the location of the to-be-relocated-object), coding distances and direction from (local or distal) landmarks in the environment (i.e. allocentric spatial updating). Children 5 to 9 years of age were tested on an object location memory task in which, between presentation and test, the availability of local cues and distal cues were manipulated. Also, participants' viewpoint could be changed. An overall performance score (i.e. absolute distance) and angular errors were obtained, with the latter providing specific insight in the use of local and/or distal landmarks for orientation. The angular errors revealed outspoken landmark effects: children performed better when the local cues were available at test, and the distal cues appeared specifically useful to help process a change of view. However, for the overall performance no such landmark effects were found. Therefore, it was concluded that the landmarks provided directional information, but did not allow location coding (i.e. distance and direction). In addition, it was shown that distal landmarks can provide orientation during a navigation task (chapter 5). Apparently, children can profit from the use of these landmarks already at the age of 5 years. Interestingly, 10-year-olds oriented themselves differently in the environment than younger children. That is, the oldest age groups oriented at the beginning of a path, whereas the younger children oriented themselves with respect to the environmental landmarks along the way. This effect indicates that distal landmark information is weighted differently in different age groups.

8.6 Conclusion

In this thesis we have presented several findings that support the adaptive combination model by Newcombe and Huttenlocher (2006, and Learmonth et al., 2008, and Newcombe & Ratliff, 2007). This model proposes that the weighting of different spatial information sources changes with age. In line with the predictions of this model it was shown that: i. children younger than 10 years weight categorical and coordinate information different than adults (chapter 2 and 3); ii. egocentric and allocentric strategies are encoded in parallel already early in life, but older children prefer to use different information sources (i.e. allocentric) compared to younger children (i.e. egocentric) (chapter 4 and 5); iii. (distal) landmark and boundary information are weighted differently in different age groups (chapter 6 and 7). Differential weighting is adaptive if it reflects developmental changes in the underlying reliabilities of the different information sources (Cheng et al., 2007), but could also indicate a failure to integrate the different sources of information at all (Nardini et al., 2008). The weights given to different information sources will depend on the certainty with which information is encoded, the salience of the information, and children's learning history. The data presented in this thesis do not allow us to address how these factors influence the weighting of different types of information. Yet, their potential theoretical implications are worth of further investigation. It can be recommended to use environments that approach ecological validity (Smith et al., 2008), e.g. experiments designed in virtual reality have advantages over traditional spatial memory paradigms in terms of their flexibility, generalizability, and experimental control (Astur et al., 2004). Also, they can be adapted for functional imaging, which, in turn, could give more direct insight in the maturation of brain areas. To conclude, the question how children learn to deal with space will not yield a simple, single answer. This thesis, if anything, has mapped the variety of cognitive mechanisms underlying spatial memory and navigation. Notably, many of them are present relatively early in life and seem to operate in parallel. Given the essential importance spatial memory and navigation have for an individual's well being, it may not be a surprise that the human brain adopted many ways to code the spatial layout of the world that early.

Samenvatting in het Nederlands

1. Samenvatting

De vaardigheid om ons in een bepaalde omgeving te kunnen oriënteren is van cruciaal belang in het dagelijks leven. Ons oriëntatievermogen helpt ons bij het bepalen van de richting die we (moeten) nemen: de navigatiestrategie. Zouden we hiertoe niet in staat zijn, dan zouden we continu op zoek zijn naar onze spullen, voortdurend de weg kwijtraken en overal tegen aanlopen. De vraag die we met behulp van experimenteel onderzoek hebben onderzocht luidt: hoe leren kinderen het vermogen zich te oriënteren, oftewel, hoe leren kinderen omgaan met ruimte? Bekend is dat er in de eerste levensjaren grote veranderingen met betrekking tot het ruimtelijk geheugen plaatsvinden. In het kader van dit proefschrift waren we vooral geïnteresseerd in de meer subtiele veranderingen die in de jaren daarna plaatsvinden: bij kinderen van 5 tot en met 12 jaar. Allereerst hebben we gekeken naar de vaardigheid van kinderen om visueel ruimtelijke informatie te verwerken, onder andere categorische en coördinate ruimtelijke relaties binnen en/of tussen objecten (zie hoofdstuk 2). Onder categorische ruimtelijke relaties verstaan we de *abstracte* relatie binnen en/of tussen objecten (bijvoorbeeld de stoel staat *links* van de tafel), terwijl onder coördinate ruimtelijke relaties de *concrete, metrische* relatie (bijvoorbeeld de stoel staat *twee meter* van de tafel) binnen en/of tussen objecten worden begrepen. Deze twee typen ruimtelijke relaties worden door verschillende hemisferen verwerkt (Kosslyn, 1987): de linker hemisfeer is met name verantwoordelijk voor de verwerking van de categorische ruimtelijke relaties, terwijl de rechter hemisfeer vooral de coördinate relaties verwerkt. Naast aandacht voor de vaardigheid van kinderen om visueel ruimtelijke relaties te verwerken, hebben we de *veranderingen* in de verwerking van deze relaties door de beide hersenhelften onderzocht. In hoofdstuk 3 hebben we gekeken naar of en hoe kinderen deze visueel ruimtelijke relaties in combinatie met andere ruimtelijke informatie (bijvoorbeeld informatie uit de beweging van het eigen lichaam) in verschillende referentie-kaders weergeven. Kinderen werden getest op een object locatie geheugentaak, bestaande uit plaatjes van kamers met daarin verschillende voorwerpen. Op sommige *trials* werd het gezichtspunt veranderd (in de tijd die verstreek tussen de presentatie van het plaatje en de uiteindelijke testsituatie). Op die manier konden we het gebruik van verschillende referentiekaders onderzoeken. In dezelfde taak hebben we gekeken of kinderen categorische en coördinate relaties na een verandering van gezichtspunt konden reproduceren. In hoofdstuk 4 hebben we onderzocht of kinderen verschillende vormen van ruimtelijke informatie -onder meer lichaamsbeweging en lokale (dichtbij) en 'distale' (veraf) *cues*) kunnen combineren om objecten te lokaliseren. Eveneens hebben we gekeken naar het gebruik van verschillende referentiekaders in een *virtual reality* navigatie taak (hoofdstuk 5). Hierbij waren we vooral geïnteresseerd in hoe het spontane gebruik van verschillende navigatiestrategieën zich met het toenemen van de leeftijd ontwikkelt. In hoofdstuk 6 hebben we vervolgens gekeken naar de invloed van ervaring op het gebruik van verschillende typen verwerking (waar we in paragraaf 4 op zullen terugkomen), gebaseerd op verschillende soorten referentiekaders. Tenslotte hebben we in hoofdstuk 7 gekeken of kinderen in staat zijn om de locatie van een object te leren in relatie tot een *landmark* of in relatie tot een *boundary*. Hierbij moesten ze zich oriënteren aan de hand van 'distale' *landmarks* in de omgeving. In de volgende paragrafen zullen we op de hoofdstukken afzonderlijk terugkomen.

2. Ontwikkeling van ruimtelijke relaties

Het '*hierarchical dual coding'* model van Huttenlocher en collega's (1991) stelt dat, om de juiste locatie van een object te onthouden, coördinate ruimtelijke relaties worden 'gewogen' met algemene categorische informatie. In twee ontwikkelingsonderzoeken met kinderen die in leeftijd varieerden van 16 maanden tot 10 jaar werd gebruik gemaakt van verschillende ruimtelijke dimensies: van een eendimensionaal vlak (Huttenlocher et al., 1994) en van twee dimensies (Sandberg et al., 1996). In deze onderzoeken werd empirisch onderzocht of kinderen deze ruimtelijke relaties inderdaad 'wegen', om op die manier de locatie van een object te kunnen onthouden. In beide onderzoeken werd een ontwikkelingsverloop geobserveerd. Het eerste onderzoek toonde aan dat het verwerken van zowel categorische als coördinate ruimtelijke relaties al vroeg aanwezig is. Het vermogen van kinderen om een eendimensionale ruimte in verschillende categorieën op te delen, verbetert echter door de jaren heen. In het tweede onderzoek werd aangetoond dat de constructie van ruimtelijke categorieën aan de hand van afstand tot een middelpunt en hoeken zich pas tussen het 7^{e} en 9^{e} levensjaar ontwikkelt. Dit zou te maken kunnen hebben met de betere verwerkingsmogelijkheden van oudere kinderen (Sandberg, 1999). Geconcludeerd werd dat jonge kinderen categorische en coördinate ruimtelijke relaties combineren om de locatie van een of meerdere objecten te onthouden, maar dat het 'gewicht' dat aan de ruimtelijke relaties wordt gegeven met het toenemen van de leeftijd verandert. In dit proefschrift hebben we onderzocht of kinderen coördinate en categorische ruimtelijke relaties verschillend 'wegen' wanneer het gezichtspunt op een plaatje van een kamer met daarin verschillende voorwerpen verandert (hoofdstuk 3). In dit onderzoek verwachtten we dat de zekerheid waarmee coördinate ruimtelijke relaties worden verwerkt, zou variëren met de grootte van de verandering in gezichtspunt. Aangezien de categorische relatie een meer abstracte relatie betreft, verwachtten we daarentegen dat dit gezichtspunteffect kleiner zou zijn voor het verwerken van de categorische ruimtelijke relaties. Daarnaast zou deze zogenaamde 'constantie' voor categorische relaties en de variatie van coördinate relaties voor kinderen van verschillende leeftijden verschillen. In tegenstelling tot onze verwachting, vonden we dat de prestatie van kinderen van 5 tot en met 10 jaar op zowel de categorische als de coördinate *trials* niet varieerden met de grootte van verandering in gezichtspunt. Wel bleek dat de kinderen over het algemeen beter op categorische *trials* dan op coordinate *trials* presteerden. Dit impliceert dat kinderen vooral op de categorische ruimtelijke relaties letten wanneer ze de locatie van verschillende voorwerpen in een kamer moesten onthouden. Op dit moment zijn we vervolgexperimenten aan het opzetten waarin volwassen proefpersonen worden getest. De voorlopige resultaten wijzen uit dat, in tegenstelling tot de resultaten van de kinderen, er steun wordt gevonden voor het 'onzekerheid met verandering in gezichtspunt' model bij volwassenen (Van der Ham et al., *in voorbereiding*). Gegeven dit feit en in overeenstemming met de resultaten van Sandberg en collega's (1996) kan worden geconcludeerd dat kinderen jonger dan 10 jaar categorische en coördinate relaties anders 'wegen' dan oudere kinderen en volwassenen (Newcombe & Huttenlocher, 2000).

Naast de functie van het goed kunnen onthouden van *waar* bepaalde objecten zich in een ruimte bevinden, is het verwerken van ruimtelijke relaties ook van belang bij het herkennen van objecten. In hoofdstuk 2 hebben we de vaardigheid van kinderen tussen de 6 en 12 jaar onderzocht om categorische en coördinate relaties binnen en tussen objecten te verwerken. Dit hebben we gedaan aan de hand van een ‘ruimtelijke relatie verandering detectietaak’ (‘herkenningstaak’). In deze taak werd kinderen gevraagd om aan te geven of het plaatje dat ze te zien kregen ‘hetzelfde’ (qua positionering van de getoonde objecten) was of ‘anders’ dan het plaatje dat ze daarvoor te zien hadden gekregen. Allereerst werd aangetoond dat 10 tot 12 jarigen en volwassenen de ruimtelijke veranderingen beter zagen dan 6 tot 8 jarigen (Huttenlocher et al., 1994; Newcombe & Huttenlocher, 2000). In tegenstelling tot de onderzoeken naar het object locatie geheugen (zoals hierboven beschreven) deden de kinderen het echter beduidend minder goed op de categorische *trials*. Een verklaring hiervoor kan zijn dat de kinderen in de ‘herkenningstaak’ een coördinate strategie voor de categorische *trials* hanteerden. De presentatietijd van de stimuli was namelijk erg kort en wellicht werd het moeilijk bevonden om in die beperkte tijd een categorisch abstract label te bedenken (Laeng, 1994; Laeng & Peters, 1995: Laeng et al., 1999). Bewijs voor deze optie werd gevonden in de hemisfeer effecten, waarin oudere kinderen (10 tot 12 jaar) en volwassenen minder ‘categorische’ fouten maakten in het linker visuele veld (= de rechter hemisfeer), waarvan wordt verondersteld dat deze verantwoordelijk is voor het verwerken van coördinate relaties (Kosslyn et al. 1989, 1992).

Samengevat is het verwerken van ruimtelijke relaties zowel belangrijk voor het onthouden van de locatie van een object (object locatie geheugen) als voor het leren en het onthouden van hoe objecten eruit zien (herkenningsgeheugen). Volgens het ‘*hierarchical dual coding*’ model worden categorische en coördinate ruimtelijke relaties verschillend ‘gewogen’. Categorische ruimtelijke relaties geven de abstracte relatie binnen en/of tussen objecten weer. Hierop zal worden teruggevallen als de tijd waarbinnen de locatie van een object moet worden onthouden langer wordt, dan wel de grootte van de verandering van gezichtspunt groter wordt (Huttenlocher et al., 1991; Postma et al., 2006). We hebben aangetoond dat kinderen, als deze tijd inderdaad lang genoeg, al op jonge leeftijd gebruik maakten van categorische relaties om de locatie van een object te onthouden.

3. Ontwikkeling van referentiekaders

Naast het verwerken van specifieke relaties waren we geïnteresseerd in of en hoe kinderen deze ruimtelijke relaties in combinatie met andere ruimtelijke informatie (bijvoorbeeld beweging) in verschillende referentiekaders weergeven. In de literatuur worden over het algemeen twee referentiekaders gedifferentieerd: één waarin de locaties van voorwerpen worden gerepresenteerd ten opzichte van iemands eigen lichaam (egocentrisch) en één waarin de locaties worden gerepresenteerd in termen van afstand en richting ten opzichte van verschillende *landmarks* en/of de geometrie van een omgeving (allocentrisch). Daarnaast is er een derde mogelijkheid, namelijk het gebruik van een ‘visueel plaatje’. Hierin worden voorwerpen opgeslagen als een geïntegreerd plaatje. Met behulp van een object locatie geheugen herkenningstaak (hoofdstuk 3) werd aangetoond dat kinderen boven kansniveau presteerden zowel in de conditie waarin zowel een egocentrisch als een allocentrisch referentiekader kon worden gebruikt als wanneer alleen een allocentrisch referentiekader kon worden gehanteerd. Aangezien de proefpersonen van te voren niet wisten welke taakconditie ze zouden ontvangen, werd geconcludeerd dat kinderen 5 tot 10 jaar de verschillende referentiekaders tegelijkertijd hadden verwerkt. Dit komt overeen met de bevinding dat bij kinderen mogelijk al op jonge leeftijd verschillende referentiekaders parallel naast elkaar kunnen opereren (Nardini et al., 2006).

4. Egocentrisch referentiekader

Binnen de verschillende referentiekaders worden verschillende manieren van ruimtelijk coderen onderscheiden: respons leren, egocentrisch ruimtelijk *updaten*, *place* leren en allocentrisch ruimtelijk *updaten*. De eerste twee vereisen een egocentrisch referentiekader, de laatste twee een allocentrisch referentiekader. Respons leren verwijst naar gedrag dat gestimuleerd wordt door de aanwezigheid van bepaalde sensorische informatie (bijvoorbeeld iemand kan een locatie direct vinden, omdat deze locatie is aangegeven met een vlag). Ook kan het verwijzen naar een beperkte opeenvolging van bewegingen (bijvoorbeeld links-rechts) (Hartley et al., 2003; Iaria et al., 2003; Packard & McGaugh, 1996; Rondi-Reig et al., 2006). Eerder onderzoek heeft aangetoond dat respons leren al vroeg in de ontwikkeling aanwezig is (Newcombe & Huttenlocher, 2000). In hoofdstuk 6 hebben we gekeken naar de invloed van ervaring op respons en *place* leren (= het verwerken van de ruimtelijke relaties tussen objecten in de omgeving). Hierbij waren we vooral geïnteresseerd in de mate waarin kinderen konden profiteren van feedback op de *place* leren taak. Zoals verwacht, vonden we geen verschillen tussen de prestaties van kinderen van 7 respectievelijk 10 jaar op de respons taak. Daarentegen vonden we tussen deze leeftijdsgroepen wel verschillen op de *place* leren taak. In paragraaf 5 komen we hier uitgebreider op terug. Een ander soort respons leren dat we hebben onderzocht, het *landmark*-gerelateerde leren, is besproken in hoofdstuk 7. Hierin was de locatie van een object geassocieerd met een lokale *landmark* en waren daarnaast ter oriëntatie de ‘distale’ *landmarks* nodig. De lokale *landmark* in dit onderzoek had, in tegenstelling tot de lokale *landmark* gebruikt in het onderzoek beschreven in hoofdstuk 6, geen interne as, dat wil zeggen de lokale *landmark* zag er aan alle kanten hetzelfde uit. Daarnaast was de locatie van het object ook niet direct verbonden aan het *landmark*. Om deze redenen dienden met name de ‘distale’ *landmarks* ter oriëntatie te worden gebruikt. We hebben *landmark*- gerelateerd leren vergeleken met *boundary*- gerelateerd leren in kinderen van 5, van 7 en volwassenen. De ronde, omsloten omgeving waarin de kinderen werden getest, was de ‘*boundary*’. Alle leeftijdsgroepen presteerden op beide leertypen boven kansniveau. Dit betekent dat alle proefpersonen de ‘distale’ *landmarks* gebruikten in combinatie met de lokale *landmark* of *boundary*. De kinderen verschilden echter van de volwassenen in de manier waarop ze de informatie ‘wogen’: de kinderen lieten hun keuzes minder beïnvloeden door de *boundary* dan de volwassenen.

Een ander soort ruimtelijk coderen, dat eveneens een egocentrisch referentiekader vereist, is egocentrisch ruimtelijk *updaten*. Dit staat voor de vaardigheid om de locatie van een object te *updaten* (bijvoorbeeld tijdens beweging) met betrekking tot onszelf. Evenals respons leren is egocentrisch ruimtelijk *updaten* al vroeg in de ontwikkeling aanwezig. Simons en Wang (1998) hebben, eind jaren negentig van de vorige eeuw, een object locatie geheugen paradigma ontwikkeld om het egocentrisch ruimtelijk *updaten* bij volwassenen te testen. Dit paradigma is later aangepast om ruimtelijk updaten te onderzoeken bij kinderen van 3 tot 6 jaar oud (Nardini et al., 2006). Het belangrijkste resultaat van zowel dit kind als volwassenenonderzoek is dat proefpersonen gezichtspuntverandering veroorzaakt door eigen beweging, prefereerden boven een gezichtspuntverandering veroorzaakt door rotatie van een configuratie van objecten. Dit resultaat kwam naar voren ondanks het feit dat deze veranderingen in dezelfde visuele informatie resulteerden. Deze bevinding suggereert inderdaad dat kinderen al op jonge leeftijd hun positie in een omgeving kunnen *updaten*.

In aansluiting hierop vonden Newcombe en collega's (1998) dat 22 maanden oude kinderen bewegingsinformatie (bijvoorbeeld egocentrisch ruimtelijk *updaten*) kunnen combineren met 'distale' *landmarks*. In hoofdstuk 4 hebben we dit onderzoek uitgebreid door de aanwezigheid van zowel lokale als 'distale' *landmarks* te manipuleren. Daarnaast hebben we de functie van de *landmarks* veranderd van een basis voor directe coding (zoals in het onderzoek van Newcombe et al, 1998) naar een basis ter oriëntatie (Hermer & Spelke, 1994; 1996). We zullen hier op terugkomen als we het gebruik van een allocentrisch referentiekader bespreken. Eveneens hebben we, zoals het paradigma van Simons en Wang en de taak van Newcombe en collega's het gezichtspunt van de kinderen veranderd door hen, tussen presentatie en test, naar een andere locatie in de testkamer te laten lopen. Uit ons onderzoek kwam naar voren dat alle kinderen boven kansniveau presteerden in de conditie waarin hun gezichtspunt veranderde, maar geen visuele *landmarks* beschikbaar waren. In overeenstemming met voorgaand onderzoek toont deze bevinding aan dat kinderen op jonge leeftijd al effectief gebruik kunnen maken van hun eigen bewegingen (egocentrisch ruimtelijk *updaten*).

In hoofdstuk 5 hebben we gekeken naar hoe het gebruik van egocentrisch ruimtelijk *updaten* (ook wel een sequentieel egocentrische strategie genoemd, Rondi-Reig et al., 2006) en allocentrisch ruimtelijk *updaten* zich met het toenemen van de leeftijd en over een serie van leer*trials* ontwikkelt. Kinderen van 5, 7 respectievelijk 10 jaar werden op een navigatietaak getest, waarin ze van verschillende strategieën gebruik konden maken. Er werd aangetoond dat kinderen van 5 jaar de voorkeur geven aan een egocentrische strategie, maar dat ze boven kansniveau presteerden als ze een allocentrische strategie moesten gebruiken. Deze bevinding suggereert dat al op jonge leeftijd kinderen beide navigatie strategieën tegelijkertijd kunnen verwerken, maar dat ze een voorkeur hebben voor het gebruik van een bepaalde strategie.

De resultaten besproken in hoofdstuk 4 en 5 zijn in overeenstemming met de bevinding van Newcombe en Huttenlocher (2000) dat ontwikkeling in het gebruik van verschillende referentiekaders gelijk staat aan veranderingen in de waarschijnlijkheid om bepaalde referentiekaders te gebruiken. Dergelijke veranderingen zijn gebaseerd op de 'gewichten' die aan bepaalde ruimtelijke informatie worden gegeven. Concluderend, zowel egocentrische als allocentrische strategieën worden al in de vroege kinderjaren tegelijkertijd verwerkt, maar oudere kinderen geven de voorkeur aan andere ruimtelijke informatie of navigatiestrategieën dan jongere kinderen.

5. Allocentrisch referentiekader

De twee types ruimtelijke *coding* waarvoor een allocentrisch referentiekader nodig is, zijn *place* leren en allocentrisch ruimtelijk *updaten*. Voor *place* leren verwerken we de ruimtelijke relaties tussen objecten in de omgeving. Zoals besproken in de introductie van dit proefschrift is de Morris water *maze* een veelgebruikt paradigma om *place* leren te onderzoeken (Morris, 1982). Recentelijk werd echter aangetoond dat dit paradigma eigenlijk meer 'richting' meet in plaats van het navigeren naar een precieze locatie in een omgeving (Hamilton et al., 2007; Hamilton et al. 2008). In twee hoofdstukken van dit proefschrift hebben we *place* leren (hoofdstuk 6) en *boundary*- gerelateerd leren (hoofdstuk 7) bij kinderen onderzocht. Zoals hierboven beschreven, hebben we in hoofdstuk 6 de ontwikkeling van respons leren en *place* leren onderzocht aan de hand van een leerparadigma. In overeenstemming met onze verwachtingen vonden we geen verschillen tussen de prestaties van kinderen van 7 respectievelijk 10 jaar op de respons taak, maar vonden we dat kinderen van 7 jaar significant slechter presteerden op de *place* taak. Een interessante observatie was dat de 7-jarigen hun prestatie wel verbeterden nadat ze feedback hadden gekregen. Het feit dat jongere kinderen (tot 8 jaar) niet 'spontaan' gebruik maakten van de 'distale' *landmarks* om de locatie van een object te onthouden (*place* leren), kan betekenen dat ze deze *landmarks* minder belangrijk vonden en er om die reden minder 'gewicht' aan gaven (Newcombe & Huttenlocher, 2000; Newcombe & Ratliff, 2007).

In hoofdstuk 7 hebben we gekeken naar de vaardigheid van kinderen om *boundary*- gerelateerd te leren. Zoals hierboven (paragraaf 4) besproken, leerden kinderen van 5, 7 respectievelijk volwassenen de associatie tussen de locatie van een object en een lokale *landmark* en de associatie tussen de locatie van een object en een *boundary*. Aangezien zowel de lokale *landmark* als de *boundary* geen interne as hadden, waren de 'distale' *landmarks* ter oriëntatie nodig. Alle leeftijds-groepen presteerden op beide leertypen boven kansniveau. Concluderend, al op jonge leeftijd kunnen kinderen afstand (van de lokale *landmark* of *boundary*) en richting informatie combineren. Deze bevinding komt overeen met onderzoek waaruit blijkt dat kinderen vanaf 18 maanden al in staat zijn om, in combinatie met geometrische informatie van de rechthoekige testkamer, *landmark* informatie te gebruiken om zich te oriënteren (Learmonth et al., 2001; Cheng & Newcombe, 2005).

In de discussie van hoofdstuk 7 veronderstellen we dat de resultaten kunnen worden verklaard door het 'adaptief wegen' van verschillende informatie (Newcombe & Huttenlocher, 2000; Newcombe & Ratliff, 2007). Een alternatieve verklaring kan echter zijn dat de kinderen moeite hadden de lokale *landmark*, de *boundary* van de omgeving en de 'distale' *landmarks* sowieso te integreren (Nardini et al., 2008). Vervolgonderzoek zou de *landmark* en *boundary* moeten isoleren om de betrouwbaarheid van beide *cues* te manipuleren en zo de houdbaarheid van beide alternatieven te onderzoeken.

In hoofdstuk 4 hebben we onderzocht of kinderen verschillende ruimtelijke informatie bronnen kunnen combineren om objecten te lokaliseren. In aanvulling op de uitgebreide literatuur over de vaardigheid van kinderen om zich in een gesloten omgeving te oriënteren (Learmonth et al., 2001; Cheng & Newcombe, 2005), waren we geïnteresseerd in hun vaardigheid om hun ruimtelijke locatie te *updaten* met behulp van afstanden en richtingen van lokale en 'distale' *landmarks* in de omgeving Dit laatste wordt ook wel allocentrisch ruimtelijk *updaten* genoemd. Kinderen van 5 tot 9 jaar werden getest op een object locatie geheugentaak waarin, tussen presentatie en test, de aanwezigheid van lokale *landmarks* en 'distale' *landmarks* werd gemanipuleerd. Daarnaast kon ook het gezichtspunt van de proefpersoon worden veranderd. Voor elk teruggeplaatst object kregen de kinderen een 'algemene prestatiescore', waarin de absolute afstandfout werd meegenomen en de richtingsfout werd gemeten. Deze laatste meting gaf een meer specifiek inzicht in het gebruik van lokale en 'distale' *landmarks* ter oriëntatie. Over het algemeen lieten de richtingsfouten van de kinderen een duidelijk landmark effect zien: kinderen presteerden beter als de lokale *landmarks* tijdens de test aanwezig waren, terwijl 'distale' *landmarks* vooral van belang leken bij een gezichtspuntverandering van de proefpersoon. Voor de 'algemene prestatiescore' werd echter geen *landmark* effect gevonden. Geconcludeerd werd dat de *landmarks* weliswaar richtinginformatie gaven, maar geen combinatie van richting en afstand (locatie *coding*). In hoofdstuk 5 werd aangetoond dat 'distale' *landmarks* oriëntatie informatie ook tijdens het navigeren kunnen geven. Kennelijk kunnen kinderen al op jonge leeftijd profiteren van het gebruik van deze *landmarks*. Een interessante bevinding in hoofdstuk 5 was voorts dat kinderen van 10 jaar zichzelf in een omgeving *anders* oriënteren dan jongere kinderen. De oudste kinderen oriënteerden zich aan het begin (i.e. vóórdat ze de route gingen lopen), terwijl de jongere kinderen zich gedurende het afleggen van de route oriënteerden. Dit effect laat zien dat 'distale' *landmark* informatie in verschillende leeftijdsgroepen *anders*, ofwel op een *ander tijdstip* wordt gewogen.

6. Conclusie

Dit proefschrift laat verschillende bevindingen zien die overeenkomen met de predicties van het 'adaptief combinatie' model zoals ontwikkeld door Newcombe en Huttenlocher (2006; Learmonth et al., 2008; Newcombe & Ratliff, 2007). Dit model stelt dat het 'wegen' van verschillende soorten ruimtelijke informatie met het toenemen van de leeftijd verandert. In overeenstemming met dit model hebben we aangetoond dat i.) kinderen jonger dan 10 jaar categorische en coördinate ruimtelijke relaties anders wegen dan oudere kinderen en volwassenen (hoofdstukken 2 en 3); ii.) egocentrische en allocentrische (navigatie)strategieën al in de vroege kinderjaren tegelijkertijd worden gebruikt, maar dat oudere kinderen de voorkeur geven aan allocentrische (omgeving) informatie, terwijl jongere kinderen de voorkeur geven aan egocentrische informatie (hoofdstukken 4 en 5); iii.) *landmark* en *boundary* informatie gedurende de ontwikkeling verschillend worden 'gewogen' (hoofdstukken 6 en 7). Dit 'wegen' adaptief als het ontwikkelingsgerelateerde veranderingen in de betrouwbaarheid van verschillende vormen van ruimtelijke informatie weergeeft (Cheng et al., 2007), maar het kan eveneens betekenen dat kinderen moeite hebben om verschillende ruimtelijke informatie sowieso te integreren (Nardini et al., 2008). De 'gewichten' die aan de verschillende vormen van ruimtelijke informatie worden toegekend hangen onder andere af van de zekerheid waarmee de informatie is verwerkt, de opvallendheid van de informatie en van de leerhistorie van de kinderen. In dit proefschrift hebben we niet gekeken naar hoe deze factoren het wegen van ruimtelijke informatiebronnen beïnvloedt. Hier zou in de toekomst onderzoek naar kunnen worden gedaan. Daarbij zou gebruik kunnen worden gemaakt van virtuele omgevingen (Smith et al., 2008). Dergelijke omgevingen hebben een voordeel boven een traditionele 'levensechte' manier van testen. Dit voordeel geldt met name voor de flexibiliteit, generaliseerbaarheid en experimentele controle (Astur et al., 2004). Ook kunnen deze omgevingen worden aangepast voor functioneel *imaging* onderzoek, dat meer inzicht kan geven in de eventuele rijping van verschillende hersengebieden. Concluderend, de in dit proefschrift centraal gestelde onderzoeksvraag (Hoe leren kinderen omgaan met ruimte?) levert geen simpel, eenduidig antwoord op. In dit proefschrift zijn verscheidene cognitieve mechanismen onderzocht die ten grondslag liggen aan het ruimtelijk geheugen en aan navigatie. Duidelijk is geworden dat de meeste mechanismen al aanwezig zijn in de vroege kinderjaren (in ieder geval vanaf 5 jaar en in sommige gevallen al eerder), maar dat de voorkeur voor bepaalde mechanismen verandert met de leeftijd. Omdat het ruimtelijk geheugen (voor het zich kunnen oriënteren) en het vermogen tot doelgerichte navigatie van essentieel belang zijn voor iemands welbevinden is het wellicht niet verwonderlijk dat het menselijk brein meerdere vaardigheden om de ruimtelijke *lay-out* van de wereld te 'representeren' al vroeg ontwikkelt.

References

Akers, K.G. & Hamilton, D.A. (2007) Comparison of developmental trajectories for place and cues navigation in the Morris water task. Developmental Psychobiology, 49, 553-564

Allen, G.L. & Ondracek, P.J. (1995) Age-sensitive cognitive abilities related to children's acquisition of spatial knowledge. Developmental Psychology, 31(6), 934-945

Arleo, A. & Rondi-Reig, L. (2007) Multimodal sensory integration and concurrent navigation strategies for spatial cognition in real and artificial organisms. Journal of Integrative Neuroscience, 6(3), 327-366

Astur, R.S., Tropp, J., Sava, S., Constable, R.T. & Markus, E.J. (2004) Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. Behavioral Brain Research, 151, 103-115

Bachevalier, J. & Beauregard, M. (1993) Maturation of medial temporal lobe memory functions in rodents, monkeys, and humans. Hippocampus, 3, 191-201

Banich, M.T. & Federmeier, K.D. (1999) Categorical and metric spatial processes distinguished by task demands and practice. Journal of Cognitive Neuroscience, 11, 153-166.

Berch, D.B. & Evans, R.C. (1973) Decision processes in children's recognition memory. Journal of Experimental Child Psychology, 16, 148-164.

Biegler, R. & Morris, R. G. M. (1993) Landmark stability is a prerequisite for spatial but not discrimination learning. Nature, 361, 631-633

Bird, C.M. & Burgess, N. (2008) The hippocampus and memory: insights from spatial processing. Nature, 9, 182-194

Bohbot, V.D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M. & Nadel, L. (1998) Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. Neuropsychologia, 36, 1217-1238

Bowerman, M. (1996) Learning how to structure space for language: A cross linguistic perspective. In Bloom, P., Peterson, M.A., Nadel, L. and Garrett, M.F. (Eds.), Language and Space 385-436 Cambridge, MA: MIT Press.

Bruyer, R., Scailquin, J. & Coibion, P. (1997) Dissociation between categorical and coordinate spatial computations: modulation by cerebral hemispheres, task properties, mode of response, and age. Brain and Cognition, 33(3), 245-277

Bullens, J. & Postma, A. (2008) The development of categorical and coordinate spatial relations. Cognitive Development, 23(1), 38-47

Burgess, N. (2006) Spatial memory: how egocentric and allocentric combine. Trends in Cognitive Sciences, 10(12), 551-557

Burgess, N. (2008) Spatial cognition and the brain. Annals of the New York Academy of Sciences, 1124, 77-97

Burgess, N., Maguire, E.A. & O'Keefe, J. (2002) The human hippocampus and spatial and episodic memory. Neuron, 35, 625-641

Burgess, N., Spiers, H.J. & Paleologou, E. (2004) Orientation manoeuvres in the dark: Dissociating allocentric and egocentric influences on spatial memory. Cognition, 94, 149-166

Byrne, P., Becker, S. & Burgess, N. (2007) Remembering the past and imaging the future : A neural model of spatial memory and imagery. Psychological Review, 114(2), 340-375

Byrne, P. & Becker, S. (2008) A principle for learning egocentric-allocentric transformation. Neural Computation, 20, 709-737

Carlesimo, G., Perri, R., Turriziani, P., Tomaiuolo, F. & Caltagirone, C. (2001) Remembering what but not where: independence of spatial and visual working memory in the human brain. Cortex, 37(4), 519 - 534

Cheng, K. & Newcombe, N.S. (2005) Is there a geometric module for spatial orientation ? Squaring theory and evidence. Psychonomic Bulletin & Review, 12(1), 1-23

Cheng, K., Shettleworth, S.J., Huttenlocher, J., & Rieser, J.J. (2007) Bayesian Integration of Spatial Information. Psychological Bulletin, 133, 625-637

Cohen, N.J. & Eichenbaum, H. (1993) Memory, Amnesia and the Hippocampal System, MIT Press

Cressant, A., Muller, R.U. & Poucet, B. (1997) Failure of centrally placed objects to control the firing fields of hippocampal place cells. The Journal of Neuroscience, 17(7), 2531-2542

Dépy, D., Fagot, J., & Vauclair, J. (1998) Comparative assessment of distance processing and hemispheric specialization in humans and baboons (papio papio). *Brain and Cognition, 38,* 165-182.

Doeller, C.F. & Burgess, N. (2008) Distinct error-correcting and incidental learning of locations relative to landmarks and boundaries. Proceedings of the National Academy of Sciences, 105(15), 5909-5914

Doeller, C.F., King, J.A. & Burgess, N. (2008) Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. Proceedings of the National Academy of Sciences, 105(15), 5915-5920

Dumas, T.C. (2005) Late postnatal maturation of excitatory synaptic transmission permits adult-like expression of hippocampal-dependent behaviors. Hippocampus, 15, 562-578

Ekstrom, A.D., Kahana, M.J., Caplan, J.B., Fields, T.A., Isham, E.A., Newman, E.L. & Fried, I. (2003) Cellular networks underlying human spatial navigation. Nature, 425, 184-187

Gabrielli, S., Rogers, Y. & Scaife, M. (2000) Young children's spatial representations developed through exploration of a desktop virtual reality scene. Education and Information Technologies, 5(4), 251-262

Ghaem, O., Mellet, E., Crivello, F., Tzourio, N., Mazoyer, B., Berthoz, A. & Denis, M. (1997) Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. Neuroreport, 8(3), 739-744.

Glosser, G., Deutsch, G.K., Cole, L.C., Corwin, J. & Saykin, A.J. (1998) Differential lateralization of memory discrimination and response bias in temporal lobe epilepsy patients. Journal of International Neuropsychological Society, 4, 502-511.

Gori, M., Del Viva, M., Sandini, G., & Burr, D. (2008) Young children do not integrate visual and haptic form information. Current Biology, 18(9), 694-698

Gouteaux, S., Thinus-Blanc, C. & Vauclair, J. (2001) Rhesus monkeys use geometric and nongeometric information during a reorientation task. Journal of Experimental Psychological: General130 (3), 505-519.

Greenough, W.T., Black, J.E. & Wallace, C.S. (1987) Experience and brain development. Child Development, 58, 539-559

Hamilton, D.E., Akers, K.G., Weisend, M.P. & Sutherland, R.J. (2007) How do room and apparatus cues control navigation in the Morris water task? Evidence for distinct contributions to a movement vector. Journal of Experimental Psychology: Animal Behavior Processes, 33(2), 100-114

Hamilton, D.E., Akers, K.G., Johnson, T.E., Rice, J.P. Candelaria, F.T., Sutherland, R.J., Weisend, M.P. & Redhead, E.S. (2008) The relative influence of place and direction in the Morris water task. Journal of Experimental Psychology: Animal Behavior Processes, 34(1), 31-53

Hart, R.A. & Moore, G.T. (1973) The development in spatial cognition: A review in Image & Environment, Downs, R.M. & Stea, D. (Eds) Aldine Pub. Co.

Hartley T, Maguire EA, Spiers HJ, Burgess N (2003) The well-worn route and the path less travelled: distinct neural bases of route following and wayfinding in humans. Neuron, 37, 877-888

Hartley, T., Trinkler, I. & Burgess, N. (2004) Geometric determinants of human spatial memory. Cognition, 94, 39-75

Haun, D.B.M., Allen, G.L. & Wedell, D.H. (2005) Bias in spatial memory: a categorical endorsement. Acta Psychologica, 118, 149-170.

Hellige, J.B., Bloch, M.I., Cowin, E.L., Lee Eng, T., Eviatar, Z. & Sergent, V. (1994) Individual variation in hemispheric asymmetry: multitask study of effects related to handedness and sex. Journal of Experimental Psychology: General, 123, 235-256.

Hellige, J.B. & Michimata, C. (1989) Categorization versus distance: hemispheric differences for processing spatial information. Memory & Cognition, 17, 770-776.

Hermer, L. & Spelke, E.S. (1994) A geometric process for spatial reorientation in young children. Nature, 370, 57-59

Hermer, L. & Spelke, E. (1996) Modularity and development: the case of spatial reorientation. Cognition, 61, 195-232

Hermer-Vazquez, L., Moffet, A. & Munkholm, P. (2001) Language, space, and the development of cognitive flexibility in humans: the case of two spatial memory tasks. Cognition, 79, 263-299

Hermer-Vazquez, L., Spelke, E. & Katsnelson, A. (1999) Sources of flexibility in human cognition: dual task studies of space and language. Cognitive Psychology, 39, 3-36.

Holdstock, J.S., Mayes, A.R., Gong, Q.Y, Roberts, N. & Kapur, N. (2005) Item recognition is less impaired than recall and associative recognition in a patient with selective hippocampal damage. Hippocampus, 15(2), 203-215

Hupbach, A. & Nadel, L. (2005) Reorientation in a rhombic environment: No evidence for an encapsulated geometric model. Cognitive Development, 20, 279-302

Huttenlocher, J. & Presson, C.C. (1973) Mental rotation and the perspective problem. Cognitive Psychology, 4, 277-299
Huttenlocher, J. & Presson, C.C. (1979) The coding and transformation of spatial information. Cognitive Psychology, 11, 375-394.
Huttenlocher, J., Hedges, L.V. & Duncan, S. (1991) Categories and particulars: prototype effects in estimating spatial location. Psychological Review, 98, 352-376.
Huttenlocher, J., Newcombe, N. & Sandberg, E.H. (1994) The coding of spatial location in young children. Cognitive Psychology, 27, 115-147.
Iaria G., Petrides, M., Dagher, A., Pike, B. & Bohbot, V.D. (2003) Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. The Journal of Neuroscience, 23(13), 5945-5952
Iglói, K., Zaoui, M., Berthoz, B. & Rondi-Reig, L. (*submitted*) Sequential egocentric strategy is acquired as early as allocentric strategy: temporal coexistence of these two navigation strategies.
Jager, G. & Postma, A. (2003) On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. Neuropsychologia, 41, 504-515.
Jansen-Osmann, P. & Fuchs, P. (2006) Wayfinding behavior and spatial knowledge of adults and children in a virtual environment. Experimental Psychology, 53(3), 171-181
Jansen-Osmann, P. & Wiedenbauer, G. (2004) The representation of landmarks and routes in children and adults: A study in a virtual environment. Journal of Environmental Psychology, 24, 347-357
Jansen-Osmann, P., Schmid, J. & Heil, M. (2007) Wayfinding behavior and spatial knowledge of adults and children in a virtual environment: the role of the environmental structure. Swiss Journal of Psychology, 66(1), 41-50
Jeffery, K.J. & O'Keefe, J.M. (1999) Learned interaction of visual and idiothetic cues in the control of place field orientation. Experimental Brain Research, 127, 151-161
Kemmerer, D. (2006) The semantics of space: Integrating linguistic typology and cognitive neuroscience. Neuropsychologia, 44, 1607-1621.
King, J.A., Burgess, N., Hartley, T., Vargha-Khadem, F. & O'Keefe, J. (2002) Human hippocampus and viewpoint dependence in spatial memory. Hippocampus, 12, 811-820
King, J.A. Trinkler, I., Hartley, T., Vargha-Khadem, F. & Burgess, N. (2004) The hippocampal role in spatial memory and the familiarity-recollection distinction: A case study. Neuropsychology, 18(3), 405-417
Klatzky, R.L. (1998) Allocentric and egocentric spatial representations: definitions, distinctions, and interconnections. Chapter prepared for a conference on Raumkognition, Trier, Germany.
Knierim, J.J., Kudrimoti, H.S. & McNaughton, B.L. (1995) Place cells, head direction cells, and the learning of landmark stability. Journal of Neuroscience, 15(3), 1648-1659
Koenig, O., Reiss, L.P. & Kosslyn, S.M. (1990) The development of spatial relation representations: evidence from studies of cerebral lateralization. Journal of Experimental Child Psychology, 50, 119-130.
Kosslyn, S.M. (1987) Seeing and imagining in the cerebral hemispheres: A computational approach. Psychological Review, 94, 148-175.
Kosslyn, S.M., Koenig, O., Barrett, A., Backer Cave, C., Tang, J. & Gabrieli, J.D.E. (1989) Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate relations. Journal of Experimental Psychology: Human Perception and Performance, 15, 723-735.
Kosslyn, S.M., Chabris, C.F., Koenig, O. & Marsolek, C.J. (1992) Categorical versus coordinate spatial relations: computational analyses and computer simulations. Journal of Experimental Psychology: Human Perception and Performance, 18, 562-577.
Kosslyn, S.M., Behrmann, M. & Jeannerods, M. (1995) The cognitive neuroscience of mental imagery. Neuropsychologia, 33, 1335-1344.
Laeng, B. (1994) Lateralization of categorical and coordinate spatial functions: a study of unilateral stroke patients. Journal of Cognitive Neuroscience, 6, 189-203.
Laeng, B. & Peters, M. (1995) Cerebral lateralization for the processing of spatial coordinates and categories in left - and right - handers. Neuropsychologia, 33, 421-439.
Laeng, B., Shah, J. & Kosslyn, S.M. (1999) Identifying objects in conventional and contorted poses: contributions of hemisphere-specific mechanisms. Cognition, 70, 53-85.
Landau, B., Gleitman, H. & Spelke, E. (1981) Spatial knowledge and geometric representation in a child blind from birth. Science, 213, 1275-1278

Landau, B., Spelke, E. & Gleitman, H. (1984) Spatial knowledge in a young blind child. Cognition, 16, 225-260

Lavanex, P., Lavenex, P.B. & Amaral, D.G. (2007) Postnatal development of the primate hippocampal formation. Developmental Neuroscience, 29, 179-192

Learmonth, A.E., Nadel, L. & Newcombe, N.S. (2002) Children's use of landmarks; Implication for modularity theory. Psychological Science, 13, 337-341

Learmonth, A.E., Newcombe, N.S. & Huttenlocher, J. (2001) Toddlers' use of metric information and landmarks to reorient. Journal of Experimental Child Psychology, 80, 225-244

Learmonth, A.E., Newcombe, N.S., Sheridan, N. & Jones, M. (2008) Why size counts: Children's spatial reorientation in large and small enclosures. Developmental Science, 11(3), 414-426

Lehnung, M. Leplow, B., Friege, L., Herzog, A. & Ferstl, R. (1998) Development of spatial memory and spatial orientation in preschoolers and primary school children. British Journal of Psychology, 89, 463-480

Lehnung, M., Leplow, B., Ekroll, V., Herzog, A., Mehdorn, M. & Ferstl, R. (2003) The role of locomotion in the acquisition and transfer of spatial knowledge in children. Scandinavian Journal of Psychology, 44, 79-86

Leplow, B., Lehnung, M., Pohl, J., Herzog, A., Ferstl, R. & Mehdorn, M. (2003) Navigational place learning in children and young adults as assessed with a standardized locomotor search task. British Journal of Psychology, 94, 299-317

MacDonald, S.E., Spetch, M.L., Kelly, D.M. & Cheng, K. (2004) Strategies in landmark use by children, adults and marmoset monkeys. Learning and Motivation, 35, 322-347

Maguire, E.A., Frackowiak, R.S.J. & Frith, C.D. (1996) Learning to find your way : A role for the human hippocampal formation. Proceedings : Biological Science, 263, 1745-1750

Maguire, E.A., Frackowiak, R.S.J. & Frith, C.D. (1997) Recalling routes around London : Activation of the right hippocampus in taxi drivers. Journal of Neuroscience, 17, 7103-7110

Maguire, E.A., Burgess, N., Donnett, J.G., O'Keefe, J. & Frith, C.D. (1998) Knowing where things are: Parahippocampal involvement in encoding object locations in virtual large-scale space. Journal of Cognitive Neuroscience, 10(1), 61-76.

Martin, P.D. & Bertoz, A. (2002) Development of spatial firing in the hippocampus of young rats. Hippocampus, 12(4), 465-480

Maurer, R. & Derivaz, V. (2000) Rats in a transparent Morris water maze use elemental and configural geometry of landmarks as well as distance to the pool wall. Spatial Cognition and Computation, 2, 135-156

May, M. (2004) Imaginal perspective switches in remembered environments: Transformation versus interference accounts. Cognitive Psychology, 48(2), 163-206.

Michimata, C. (1997) Hemispheric processing of categorical and coordinate spatial relations in vision and visual imagery. Brain and Cognition, 33, 370-387.

Milner, A.D., Dijkerman, H.C. & Carey, D.P. (1999) Visuospatial processing in a case of visual form agnosia. In Burgess, N., Jeffery, K.J. & O'Keefe, J.O. (Eds), The hippocampal and parietal foundations of spatial cognition, p.443-466. Oxford, UK : Oxford University Press.

Morris, R.G.M. (1981) Spatial localization does not require the presence of local cues. Learning and Motivation, 12, 239-260

Morris, R.G.M., Garrud, P., Rawlins, J.N.P. & O'Keefe, J. (1982) Place navigation impaired in rats with hippocampal lesions. Nature, 297, 681-683

Mou, W., McNamara, T.P., Valiquette, C.M. & Rump, B. (2004) Allocentric and egocentric updating of spatial memories. Journal of Experimental Psychology: Learning, Memory, and Cognition, 28(1), 162-170.

Nadel, L. & Hardt, O (2004) The Spatial Brain. New York: Academic Press

Nardini, M., Burgess, N., Breckenridge, K. & Atkinson, J. (2006) Differential developmental trajectories for egocentric, environmental and intrinsic frames of reference in spatial memory. Cognition, 101, 153-172

Nardini, M., Atkinson, J. & Burgess, N. (2008a) Children reorient using the left/right sense of coloured landmarks at 18-24 months. Cognition, 106, 519-527

Nardini, M., Jones, P., Bedford, R. & Braddick, O. (2008b) Development of cue integration in human navigation. Current Biology, 18, 689-693

Newcombe, N., Huttenlocher, J., Bullock Drummey, A. & Wiley, J.G. (1998) The development of spatial location coding: Place learning and dead reckoning in the second and third years. Cognitive Development, 13, 185-200

Newcombe, N.S. & Huttenlocher, J. (2000) Making Space: The Development of Spatial Representation and Reasoning. Cambridge, MA: MIT Press.

Newcombe, N.S. & Huttenlocher, J. (2006) Development of Spatial Cognition. In Handbook of Child Psychology, Volume 2: Cognition, Perception & Language (6^{th} Ed.), ed. Kuhn, D. & Siegler, R.S. John Wiley and Sons

Newcombe, N.S. & Lloyd, M.E. & Ratliff, K.R. (2007) Development of Episodic and Autobiographical Memory: A Cognitive Neuroscience Perspective. Chapter to appear in R.V. Kail (Ed.), Advances in Child Development and Behavior, Volume 35. San Diego, CA: Elsevier.

Newcombe, N.S. & Ratliff, K.R. (2007) Explaining the development of spatial reorientation: Modularity plus-language versus the emergence of adaptive combination. In The Emerging Spatial Mind (p. 53-76), ed. Plumert, J. & Spencer, J. Oxford University Press

Niebauer, C.L. (2001) A possible connection between categorical and coordinate spatial relation representations. Brain and Cognition, 47, 434-445

O'Keefe, J. (1976) Place units in the hippocampus of the freely moving rat. Experimental Neurology, 51, 78-109

O'Keefe, J. & Burgess, N. (1996) Geometric determinants of the place fields of hippocampal neurons. Nature, 381(6581), 425-428

O'Keefe, J. & Dostrovsky, J. (1971) The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely moving rat. Experimental Brain Research, 34, 171-175

O'Keefe, J. & Nadel, L. (1978) The hippocampus as a cognitive map. Oxford: Clarendon Press

O'Keefe, J. & Speakman, A. (1987) Single unit activity in the rat hippocampus during a spatial memory task. Experimental Brain Research, 68(1), 1-27.

Ono, T., Nakamura, K., Fukuda, M. & Tamura, R. (1991) Place recognition responses of neurons in monkey hippocampus. Neuroscience Letters, 121(1-2), 194-198

Ono, T., Nakamura, K., Nishijo, H. & Eifuku, S. (1993) Monkey hippocampal neurons related to spatial and nonspatial functions. Journal of Neurophysiology, 70(4), 1516-1529

Overman, W.H., Bachevalier, J., Miller, M. & Moore, K. (1996a) Children's performance on "animal tests" of oddity: implications for cognitive processes required for tests of oddity and delayed nonmatch to sample. Journal of Experimental Child Psychology, 62, 223-242

Overman, W.H., Pate, B.J., Moore, K. and Peuster, A. (1996b) Ontogeny of place learning in children as measured in the radial arm maze, Morris search task, and open field task. Behavioral Neuroscience, 110(6), 1205-1228

Packard, M.G. & McGaugh, J.L. (1992) Double dissociation of fornix and caudate nucleus lesions on acquisition of two water maze tasks: Further evidence for multiple memory systems. Behavioral Neuroscience, 106(3), 439-446

Packard, M.G. & McGaugh, J.L. (1996) Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. Neurobiology of Learning and Memory, 65, 65-72

Parrot, M., Doyon, B., Démonet, J-F. & Cardebat, D. (1999) Hemispheric preponderance in categorical and coordinate visual processes. Neuropsychologia, 37, 1215-1225.

Parslow, D.M., Rose, D., Brooks, B., Fleminger, S., Gray, J.A., Giampietro, V., Brammer, M.J., Williams, S., Gasston, D., Andrew, C., Vythelingum, G.N., Loannou, G., Simmons, A. & Morris, R.G. (2004) Allocentric spatial memory activation of the hippocampal formation measured with fMRI. Neuropsychology, 18 (3), 450-461

Pearce, J.M., Roberts, A.D.L. & Good, M. (1998) Hippocampal lesion disrupt navigation based on cognitive maps but not heading vectors. Nature, 396, 75-77

Pentland, L.M., Anderson, V.A. Dye, S. & Wood, S.J. (2003) The nine box maze test: a measure of spatial memory development in children. Brain & Cognition, 52, 144-154

Péruch, P. & Wilson, P.N. (2004) Active versus passive learning and testing in a complex outside built environment. Cognitive Processing, 5, 218-227

Piaget, J. & Inhelder, B. (1948) The Child's Conception of Space. New York: Norton

Plumert, J.M. & Hund, A.M. (2001) The development of memory for location: what role do spatial prototypes play? Child Development, 72(2), 370-384

Poldrack, R.A., Clark, J., Paré-Blagoev, E.J., Shohamy, D., Creso Moyano, J., Myers, C. & Gluck, M.A. (2001) Interactive memory systems in the human brain. Nature, 414, 546-550

Postma, A. & Laeng, B. (2006) New insights in categorical and coordinate processing of spatial relations. Neuropsychologia, 44, 1515-1518.

Postma, A., Huntjens, R.J.C., Meuwissen, M. & Laeng, B. (2006) The time course of spatial memory processing in the two hemispheres. Neuropsychologia, 44, 1914-1918.

Postma, A., Kessles, R.P.C. & Van Asselen, M. (2008) How the brain remembers and forgets where things are : The neurocognition of object-location memory. Neuroscience and Biobehavioral Reviews, 32, 1339-1345

Ratliff, K. R. & Newcombe, N.S. (2005) Human spatial reorientation using dual task paradigms. In Proceedings of the 27th Annual Meeting of the Cognitive Science Society

Ratliff, K.R. & Newcombe, N.S. (2008) Is language necessary for human spatial reorientation? Reconsidering evidence from dual task paradigms. Cognitive Psychology, 56, 142-163.

Reese, C.J. & Stiles, J. (2005) Hemispheric specialization for categorical and coordinate spatial relations during an image generation task: evidence from children and adults. Neuropsychologia, 43, 517-529.

Rondi-Reig, L., Petit, G.H., Tobin, C., Tonegawa, S., Mariani, J. & Berthoz, A. (2006) Impaired sequential egocentric and allocentric memories in forebrain-specific-NMDA receptor knock-out mice during a new task dissociating strategies of navigation. The Journal of Neuroscience, 26(15), 4071-4081

Rotenberg, A. & Muller, R.U. (1997) Variable place-cell coupling to a continuously viewed stimulus: evidence that the hippocampus acts as a perceptual system. Philosophical Transactions of the Royal Society B: Biological Sciences, 352, 1505-1513

Rybash, J.M. & Hoyer, W.J. (1992) Hemispheric specialization for categorical and coordinate spatial representations: a reappraisal. Memory & Cognition, 20, 271-276.

Sandberg, E.H. (1999) Cognitive constraints on the development of hierarchical spatial organizational skills. Cognitive development, 14, 597-619

Sandberg, E.H. & Huttenlocher, J. (1996) The development of hierarchical representation of two dimensional space. Child Development, 67, 721-739

Sergent, J. (1991) Judgements of relative position and distance on representations of spatial relations. Journal of Experimental Psychology: Human Perception and Performance, 17, 762-780.

Shelton, A.L. & Gabrieli, J.D.E. (2004) Neural correlates of individual differences in spatial learning strategies. Neuropsychology, 18(3), 442-449

Shonkoff, J.P. & Philips, D.A. (Eds.) (2000) From Neurons to Neighborhoods: The Science of Early Childhood Development. Washington, D.C.: National Academy Press

Snodgrass, J.G. & Corwin, J. (1988) Pragmatics of measuring recognition memory: applications to dementia and amnesia. Journal of Experimental Psychology: General, 117, 34-50.

Simons, D.J. & Wang, R.F. (1998) Perceiving real-world viewpoint changes. Psychological Science, 9(4), 315-320

Sluzenski, J., Newcombe, N.S. & Satlow, E. (2004) Knowing where things are in the second year of life: Implications for hippocampal development. Journal of Cognitive Neuroscience, 16, 1443-1451

Smith, A.D., Gilchrist, I.D., Cater, K., Ikram, N., Nott, K. & Hood, B.M. (2008) Reorientation in the real world: The development of landmark use and integration in a natural environment. Cognition, 107, 1102-1111

Spelke, E.S. (1998) Nativism, empiricism, and the development of knowledge. Infant Behavior and Development, 21(2), 181-200

Spiers, H.J., Burgess, N., Hartley, T., Vargha-Khadem, F. & O'Keefe, J. (2001) Bilateral hippocampal pathology impairs topographical and episodic memory but not visual pattern matching. Hippocampus, 11, 715-725.

Stanton, M.E. (2000) Multiple memory systems, development and conditioning. Behavioral Brain Research, 110, 25-37

Taube, J.S. (1998) Head direction cells and the neurophysiological basis for a sense of direction. Progress in Neurobiology, 55, 225-256

Taylor, K.J., Henson, R.N.A. & Graham, K.S. (2007) Recognition memory for faces and scenes in amnesia: Dissociable roles of medial temporal lobe structures. Neuropsychologia, 45, 2428-2438

Tolman, E. C., Ritchie, B.F. & Kalish, D. (1946) Studies in spatial learning: II. Place learning versus response learning. Journal of Experimental Psychology, 36, 221-229

Van Asselen, M., Kessels, R.P.C., Kappelle, L.J. and Postma, A. (2008) Categorical and coordinate spatial representations within object-location memory. Cortex, 44, 249 - 256

Van der Ham, I.J.M., Bullens, J., de Goede, M. & Postma, A. (*in preparation*) Categorical and coordinate spatial relations from different viewpoints in an object location memory task

Wang, R.F. (2004) Action, verbal response and spatial reasoning. Cognition, 94, 185-192.

Wang, R.F. & Simons, D.J. (1999) Active and passive scene recognition across views. Cognition, 70, 191-210

Wang, R.F. & Spelke, E.S. (2002) Human spatial representation: Insights from animals. Trends in Cognitive Science, 6(9), 376-382.

White, N.M. & McDonald, R.J. (2002) multiple parallel memory systems in the brain of the rat. Neurobiology of Learning and Memory, 77, 125-184

Wilkinson, D. & Donnelly, N. (1999) The role of stimulus factors in making categorical and coordinate spatial judgments. Brain & Cognition, 39(3), 171-185

Wilton, L.A.K., Baird, A.L., Muir, J.L., Honey, R.C. & Aggleton, J.P. (2001) Loss of the thalamic nuclei for "head direction" impairs performance on spatial memory tasks in rats. Behavioral Neuroscience, 115(4), 861-869

Windmann, S., Daum, I. & Güntürkün, O. (2002a) Dissociating prelexical and postlexical processing of affective information in the two hemispheres: effects of the stimulus presentation format. Brain and Language, 80, 269-286

Windmann, S., Urbach, T.P. & Kutas, M. (2002b) Cognitive and neural mechanisms of decision biases in recognition memory. Cerebral Cortex, 12, 808-817

Wraga, M., Creem, S.H. & Proffit, D.R. (2000) Updating displays after imagined object and viewer rotations. Journal of Experimental Psychology: Learning, Memory, and Cognition, 26, 151-168

International publications

Bullens, J. & Postma, A. (2008) The development of categorical and coordinate spatial relations. Cognitive Development, 23(1), 38-47

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. (*in press*) The role of landmarks and boundaries in the development of spatial memory. Developmental Science

Manuscripts submitted or in preparation

Bullens, J., Székely, E., Vedder, A. & Postma, A. (submitted) The effect of feedback on children's ability to show response and place learning.

Bullens, J. & Postma, A. (submitted) The role of local and distal landmarks in the development of object location memory.

Bullens, J., Igloi, K., Berthoz, A., Postma, A & Rondi-Reig, L. (in preparation) The spontaneous use of navigation strategies in children 5, 7 and 10 years of age.

Bullens, J., Van der Ham, C.J.M., De Goede, M. & Postma, A. (submitted) Children' s use of spatial reference frames and spatial relations in a scene recognition task.

Van der Ham, C.J.M., **Bullens, J.**, De Goede, M. & Postma, A. (in preparation) Categorical and coordinate spatial relations from different viewpoints in an object location memory task.

Nijboer, T., Van der Smagt, M., **Bullens, J.**, De Haan, E. & Van Zandvoort, M. (in preparation) Distinct trajectories for acquisition of colour terms and object-colour associations.

Published Abstract

Bullens, J. & Postma, A. (2007) The perception of categorical and coordinate spatial changes in children Cognitive Processing, 7(1), 152

Oral presentations

Bullens, J. & Postma, A. (2005) The development of spatial cognition: Preliminary results on a perceptual spatial information task. Wayfinding consortium meeting in Rome, Italy.

Bullens, J. & Postma, A. (2005) The perception of categorical and coordinate spatial changes in children. NVP 10th winter conference in Egmond aan Zee, the Netherlands.

Bullens, J. & Postma, A. (2006) The processing of categorical and coordinate spatial changes in children. Wayfinding consortium meeting in Paris, France.

Bullens, J. & Postma, A. (2006) The perception of categorical and coordinate spatial changes in children. International Conference on Spatial Cognition in Rome, Italy

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. (2007) The processing of landmarks and boundaries and children. Wayfinding consortium meeting, Tübingen.

Bullens, J. & Postma, A. (2007) The development of categorical and coordinate spatial change detection. 6th Dutch Endo-Neuro-Psycho Meeting in Doorwerth, the Netherlands.

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. (2007) The role of landmarks and boundaries in the development of object location memory. European Workshop on Imagery & Cognition in Utrecht, the Netherlands.

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. (2007) Children's memory for locations defined by a single landmark or boundary. The European Society for Cognitive Psychology in Marseille, France.

Bullens, J., Székely, E., Vedder, A. & Postma, A. (2007) Children's ability to use proximal and distal landmarks in order to memorize an object's location. Wayfinding consortium meeting in London, United Kingdom.

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. (2007) 'Stabiele en flexibele omgevingsfactoren in de ontwikkeling van het oriëntatievermogen bij kinderen'. NVN symposium ruimtelijke cognitie in Nijmegen, the Netherlands.

Bullens, J., Nardini, M., Doeller, C.F., Braddick, O., Postma, A. & Burgess, N. (2007) Children's ability to use stable and flexible cues in order to memorize an object's location. NVP 11th winter conference in Egmond aan Zee, the Netherlands.

Bullens, J. & Postma, A. (2008) The role of landmarks in the development of object location memory. Conference on Research and Training in Spatial Intelligence in Evanston, USA.

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Jessie Bullens was born on September 15th, 1980 in Leiderdorp, the Netherlands. In 1998 she completed her secondary education at the R.K. Alverna College in Leiden after which she studied at the Orange Coast College in California (USA) for a year. In this year she took several courses, with a major in psychology. In 1999 she started studying psychology at the University of Amsterdam. For her clinical internship she worked at the forensic institute (FORA) for six months, after which she received her diagnostic certification (BAPD). To obtain her master's thesis she did a research internship at the University of Pittsburgh (USA), where she investigated decision-making behavior in early adolescent boys with internalizing and externalizing disorders. In April 2005 she attained her master's degree, specializing in clinical -and developmental psychology. At the same time she started her PhD research project on 'the development of spatial cognition' at the Department of Experimental Psychology at Utrecht University. This research was part of a three-years funded European project 'Finding your way in the world - on the neurocognitive basis of spatial memory and orientation in humans'. Within the *Wayfinding* consortium she collaborated with the Department of Experimental Psychology at Oxford University and the Institute of Cognitive Neuroscience at University College London, for which she carried out research at the Visual Development Unit in Oxford for three months. In addition, she collaborated with the UMR-CNRS at Collège de France and UPMC-CNR Université Jussieu in Paris, France. At the moment she has a temporary position as teacher / researcher at Utrecht University.

Jessie Bullens werd geboren op 15 september 1980 te Leiderdorp. In 1998 behaalde ze het VWO diploma aan de R.K. Scholengemeenschap Alverna in Leiden, waarna ze voor een jaar ging studeren aan het Orange Coast College in Californië (VS). In dit jaar volgde ze verschillende vakken, met een specialisatie in psychologie. In 1999 startte zij haar studie psychologie aan de Universiteit van Amsterdam. Voor haar klinische stage werkte ze zes maanden bij FORA, een onafhankelijk extern deskundigen bureau dat op verzoek van justitiële instanties diagnostisch onderzoek doet bij kinderen tot 18 jaar. Middels deze stage behaalde ze haar basisaantekening psychodiagnostiek (BAPD). Haar doctoraal thesis voerde ze uit aan de University of Pittsburgh (VS), waar ze onderzoek deed naar het beslissingsgedrag van adolescente jongens (12-14 jaar) met een internaliserende en/of externaliserende stoornis. In april 2005 studeerde zij af met de specialisatie klinische ontwikkelings-psychologie. Tegelijkertijd begon ze haar promotieonderzoek naar 'de ontwikkeling van het ruimtelijk geheugen' op de afdeling Psychologische Functieleer van de Universiteit Utrecht. Het onderzoek werd verricht in het kader van een drie jaar durend Europees project '*Finding your way in the world - on the neurocognitive basis of spatial memory and orientation in humans*'. Binnen dit *Wayfinding* project heeft ze samengewerkt met het Department of Experimental Psychology aan Oxford University en het Institute of Cognitive Neuroscience aan University College London, waarvoor ze drie maanden onderzoek deed bij de Visual Development Unit in Oxford. Daarnaast heeft ze samengewerkt met het UMR-CNRS aan het Collège de France en UPMC-CNR Université Jussieu in Parijs, Frankrijk. Op dit moment heeft ze een tijdelijke positie als docent / onderzoeker aan de Universiteit Utrecht.