



Embodiment of and Individual Proclivities for Egocentric and Allocentric Reference Frames

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13 Embodiment of Spatial Reference Frames and Individual Differences in
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15 Reference Frame Proclivity
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EMBODIMENT OF SPATIAL REFERENCE FRAMES

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Abstract

Spatial cognitive processes can be based on distinct reference frames centered on the body (egocentric reference frame) or centered on aspects of the surrounding environment independent of the position and orientation of the cognizing subject (allocentric reference frame). Updating of spatial information based on an egocentric reference frame is often believed to be highly automatic while the computation of spatial information based on an allocentric reference frame is assumed to be effortful and dependent on prior egocentric space processing. In this position paper I will review theoretical and empirical work that challenges the view of such a hierarchical organization of spatial reference frames and propose an embodied view of spatial reference frame computation. This perspective is based on three interdependent aspects of spatial reference frames. First, based on the existence of neural structures that allow for an automatic computation of both, egocentric and allocentric spatial representations, a functional equivalence of distinct reference frames is proposed. Second, based on the assumption of efficient computation and parallel accessibility of distinct reference frames individual proclivities are proposed to develop based on environmental and socio-cultural influences. Finally, it is proposed that ontogenetic differences are manifest in anatomical changes associated with the dominant use of different reference frames. These changes influence the microgenesis of spatial knowledge and influence behavior in other spatial cognitive tasks. In conclusion, an embodied framework of spatial reference frames strongly suggests consideration of individual reference frame proclivities to gain further insights into the complex architecture of human spatial cognition. More importantly, neuroscientific approaches describing cortical networks and associated brain dynamics have to allow participants to actively move and behave in their environment to allow for investigating the cognitive processes and brain dynamics underlying embodied spatial

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3 cognition.

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6 Introduction

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8 Spatial orientation is a complex cognitive function that allows for a wide variety of
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10 interactions with our environment. These range from exploring new territories without getting
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12 lost to performing fast and automated spatial maneuvers based on stimulus-response associations
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14 in well-learned surroundings. During spatial orienting humans use a multitude of information
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16 from several senses including but not limited to vision, audition, the vestibular system, and
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18 kinesthesia. All these different sources inform human navigators about their movement in the
19
20 outside world as well as changes in position and orientation with respect to aspects of the
21
22 environment. This information is further integrated and coordinated with action plans and the
23
24 behavior of other social agents. While this appears to be an effortless endeavor for human and
25
26 animal navigators the complexity of the underlying spatial cognitive processes becomes obvious
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28 when orientation fails because of impairments of the underlying neural substrate (Aguirre &
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30 D'Esposito, 1999), because of ambiguity in the environment or bad wayfinding instruction
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32 (Waller, Montello, Richardson, & Hegarty, 2002), or when completely different spatial strategies
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34 lead to comparable orientation performance (Gramann, Muller, Eick, & Schonebeck, 2005). One
35
36 of the most commonly observed differences in spatial cognitive behavior might be the use of
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38 maps (Lobben, 2004). While one group of navigators physically turns the map to align it with
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40 their actual heading in the real world a second group mentally rotates themselves to bring their
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42 actual heading in agreement with the north-south orientation of the map. Both strategies can be
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44 successful but differ fundamentally with respect to the underlying cognitive processes.
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53 Here, I will review research on individual differences in spatial orientation based on the
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55 use of distinct reference frames. The review focuses on the neural mechanisms underlying the
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3 computation of distinct reference frames in humans and other species, the cultural and
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5 geographical influences on individual proclivities to use distinct reference frames, and on
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7 ontogenetic differences of reference frame proclivities that are accompanied by and expressed in
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9 cortical changes. While this review is by no means exhaustive and does not cover sex differences
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11 in spatial cognition it makes a strong point for a more careful consideration of individual
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13 differences in spatial cognitive processing in general, and specifically, for a cautious
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15 interpretation of results from imaging studies describing the neural basis of spatial cognitive
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17 processes.
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Spatial Representations and Underlying Reference Frames

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27 In the example of the city map above two different spatial strategies can be applied to
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29 solve the same problem, i.e. updating of one's own position and orientation with respect to a
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31 symbolic representation of the environment versus updating the representation of an environment
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33 with respect to one's own position and orientation. The important difference between these two
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35 strategies is the reference frame that is used to update the navigators' current position and
36
37 orientation. A spatial reference frame can be defined as a means to represent entities in space
38
39 (Klatzky, 1998) while the term strategy is defined as the use of distinct reference frames, or the
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41 use of a combination of distinct reference frames for cognitive ends. There are at least two
42
43 distinct spatial reference frames that can be distinguished based on the origin of the underlying
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45 coordinate system and the information that is stored in the resultant spatial representation: an
46
47 egocentric reference frame and an allocentric reference frame. An egocentric reference frame has
48
49 an origin based on the navigator's body and represents entities in the environment with respect to
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51 the current position and orientation of the navigator. In contrast, an allocentric reference frame
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3 has an origin outside the navigator and represents entities in space independent of the momentary
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5 position and orientation of the navigator (for extensive discussion see Klatzky, 1998). While this
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7 conceptual dichotomy makes it easier to dissociate qualitatively different spatial processes, it is
8
9 reasonable to assume that there are more than two representations active during spatial
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11 orientation. One prominent example of parallel spatial representations is the model of Redish and
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13 Touretzky (Redish & Touretzky, 1997; Touretzky & Redish, 1996). In their model animal
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15 navigation is explained by four interacting spatial representations. The *local view* representation
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17 provides the relationship of the animal to visible landmarks and is based on an egocentric
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19 reference frame. A second, egocentrically based representation, the *path integrator*, provides a
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21 direct trajectory back to the starting point of travel. The *place code*, an allocentric representation
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23 indicates the location of the animal in an environment based on place cells located in the
24
25 hippocampus, and finally, the *head direction* representation stores information with respect to the
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27 movement direction of the animal in an allocentric reference frame. Integrating information from
28
29 all four spatial representations with a goal selection subsystem allows the animal to successfully
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31 navigate in new and well-known environments (Redish & Touretzky, 1997).
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39 More importantly, while there is physiological evidence for the parallel computation of at
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41 least three different allocentric spatial reference frames in the mammalian brain (i.e., heading
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43 direction, place cells, and grid cells; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006;
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45 Moser & Moser, 2008; Taube, 1998) research in the fields of Cognitive Psychology and
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47 Geography mainly focuses on the distinction between an egocentric ‘sensorimotor’
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49 representation of space and an allocentric ‘map-like’ representation of space. Such an approach
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51 fosters conceptual reduction of representational systems and limits the development of theories
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53 explaining complex spatial behaviors in humans. One example for such a simplification is the
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3 approach to explain the genesis of spatial knowledge in humans. A well-established theory of
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5 spatial learning in children assumes an ontogenetic sequence from egocentric to allocentric
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7 representations of space implying a sequential development from basic and coarse to advanced
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9 and complex spatial representations (Piaget & Inhelder, 1967). During the first months when
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11 infants are more or less stationary in their environment they are assumed to use a sensorimotor
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13 representation (egocentric reference frame). Then, with onset of locomotion (crawling), a
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15 qualitative shift from sensorimotor to map-like (egocentric to allocentric coding) is proposed that
16
17 helps infants to keep track of their position in the environment (Acredolo, 1990; Thelen & Smith,
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19 1994).

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21
22 This concept of a developmental sequence from egocentric to allocentric spatial
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24 representations has been extended to a more general three-stage model of spatial knowledge
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26 acquisition in new environments (Hazen, Lockman, & Pick, 1978; Siegel & White, 1975).
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28 According to this framework of spatial microgenesis the first stage of spatial knowledge entails a
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30 representation of *landmarks*. Landmarks are prominent enduring features that define a specific
31
32 spatial location of the perceiving navigator and are thus based on an egocentric reference frame.
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34 In the second stage, through repetitive travel, *route knowledge* develops connecting previously
35
36 learned landmarks. The underlying reference frame is egocentric in nature providing a
37
38 representation of sensorimotor sequences that allow the navigator to reach one landmark while
39
40 being located at another (e.g., when stepping out of the train station, go straight ahead for two
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42 blocks and then turn left and you will see the cathedral). Finally, the connection of different
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44 routes into a two-dimensional map-like array defines *survey knowledge*, an allocentric spatial
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46 representation allowing for shortcuts and detours. This model explains a wide range of findings
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48 implying a hierarchy of spatial representations with a functionally superior (*superiority*
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3 *assumption*) allocentric representation preceded by and based on (*dependence assumption*) an
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5 egocentric spatial representation. Such a map-like allocentric representation is thought to allow
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7 more flexible spatial behaviors and is proposed in several models (e.g., Golledge & Spector,
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9 1978; Siegel & White, 1975).

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13 However, there is good reason to question the assumptions of *superiority* and *dependence*
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15 of allocentric over egocentric spatial representations. Theoretical and empirical evidence
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17 suggests a parallel development of egocentric and allocentric spatial knowledge for both, the
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19 ontogenesis and microgenesis of spatial knowledge [insert Footnote 2 here](e.g., Graziano &
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21 Gross, 1994; Haith & Benson, 1998; Ishikawa & Montello, 2006; Mou, McNamara, Valiquette,
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23 & Rump, 2004; Newcombe & Huttenlocher, 2003). Experimental results support the assumption
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25 that allocentric spatial representations are simply one specific form of spatial representations that
26
27 do not require effortful computation and are just as basic for spatial orienting as egocentric
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29 representations of space.
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34 Here, I will develop and discuss three general and interconnected hypotheses describing
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36 the embodiment of spatial reference frames. First, it is assumed that the mammalian brain
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38 provides a neural basis to compute several egocentric and allocentric reference frames in parallel.
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40 That is, the neural basis allowing for a computation of distinct spatial representations is soft-
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42 wired. Secondly, these genetically pre-specified neural circuits need specific inputs for
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44 maturation. Such inputs are to a certain extent coupled to the development of the navigators'
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46 physical structure and thus the ability for movement in space. In addition, specific aspects of the
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48 environment (socio-cultural as well as geographical) will influence the reference frame used.
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50 Third and finally, successful use of a specific reference frame (or class of reference frames) over
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52 the time course of individual development is associated with a proclivity to use a specific
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EMBODIMENT OF SPATIAL REFERENCE FRAMES

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reference frame. This proclivity for a specific reference frame is associated with structural changes in the cortical networks underlying the computation of the specific reference frame. In the following I will develop each of the three hypotheses, providing a theoretical as well as anatomical basis.

Soft-Wired Computation of Spatial Reference Frames

Spatial reference frames are embodied in the sense that the computation of spatial representations is based on genetically determined neural structures that code spatial information based on egocentric or allocentric reference frames. These soft-wired neural structures are plastic and can change dependent on environmental and individual influences. Sensory information (e.g., optic flow perceived while walking) is encoded based on an egocentric reference frame that is anchored in the respective sensory system (e.g., the retina). Visually coded spatial information represents a specific perspective that is dependent on the navigators' position and orientation in the environment. Changes in egocentrically coded visual information can be used for the automatic updating of position (Riecke, Cunningham, & Bulthoff, 2007). Visual, vestibular and kinesthetic information is used not only in an automated manner (i.e., efficient in the sense that no attention is needed) for spatial processing but any attempt to ignore this sensory information is computationally effortful and prone to error, both for biomechanical cues (Farrell & Robertson, 1998; but see Waller, et al., 2002) and visual cues (Riecke, et al., 2007). The neural structures that allow for an automatic processing of egocentric information are located in the primary and secondary sensory cortices. The parietal cortex provides the neural basis for integrating information embedded in distinct egocentric as well as egocentric and allocentric reference frames (Andersen & Buneo, 2002; Andersen, Snyder, Bradley, & Xing, 1997).

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Perceptual processes are closely linked to egocentric reference frames. However, the use of egocentric reference frames to represent space is not restricted to the processing of sensory information but is also found to be involved in spatial memory processing and spatial updating. When human navigators learn large-scale environments and subsequently have to retrieve information from their mental representation, landmarks that were learned to be in front of the navigator are located faster than landmarks located behind the navigator (Bryant & Tversky, 1999; Sholl, 1987). In general, the initial orientation of a navigator while learning a specific environment leads to an alignment of objects retrieved from memory along the axis experienced during learning (McNamara, Sluzenski, & Rump, 2008; McNamara, Rump, & Werner, 2003; Mou & McNamara, 2002; Shelton & McNamara, 1997; Waller, et al., 2002; Wang et al., 2006). However, while spatial memory relies on egocentric reference frames it certainly also uses representations of space that are based on allocentric reference frames representing slopes or the general geometry of an environment (Landau & Lakusta, 2009; Proffitt, Bhalla, Gossweiler, & Midgett, 1995; Steck, Mochnatzki, & Mallot, 2003), or the configuration of landmarks (McNamara, et al., 2008; McNamara, et al., 2003; Mou, Liu, & McNamara, 2009). In addition, spatial updating, i.e. the continuous updating of one's own relation to other entities in space during locomotion, also relies to a certain extent on egocentric reference frames (Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Mou, McNamara, Valiquette, & Rump, 2004). Thus, egocentric reference frames are not simply tied to sensory systems but play an important role for higher order spatial cognitive processes allowing for fast and efficient retrieval and updating of egocentrically coded information.

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Coding of spatial information in an allocentric frame of reference is also fast and efficient due to its 'soft-wired' implementation on the neural level. As a consequence, allocentric

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3 representations of space can be computed from the very first encounter with an environment and
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5 do not depend on the prior existence of egocentric spatial representations. The computation of
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7 heading is one example for an efficient allocentric coding of space. Head direction cells fire
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9 selectively when a navigator faces a specific direction. They can be controlled by prominent
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11 landmarks (but remain direction-specific in the absence of vision), and are updated by angular
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13 movement of the navigator (Taube, Muller, & Ranck, 1990a, 1990b). These characteristics allow
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15 for computing changes in heading based on body movements and thus reflect allocentric heading
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17 computation even in the absence of prominent visual landmarks. When participants have to
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19 estimate the position of objects at different eccentricities after heading changes they tend to
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21 reference space to a pre-rotatory straight ahead using internal estimates of eye, head, and trunk
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23 displacements (Mergner, Nasios, Maurer, & Becker, 2001). Influences of the navigator's initial
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25 heading orientation can be found in path integration experiments (Gramann, et al., 2005;
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27 Gramann, Muller, Schonebeck, & Debus, 2006; Gramann et al., 2010) and memory for scenes
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29 and object arrays (McNamara, et al., 2003; Mou, Xiao, & McNamara, 2008; Mou, Zhang, &
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31 McNamara, 2009). The neural structures allowing for heading computation comprise *head*
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33 *direction cells* residing in the limbic system and other cortical structures in rodents (Chen, Lin,
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35 Green, Barnes, & Mcnaughton, 1994; Fetsch, Wang, Gu, DeAngelis, & Angelaki, 2007;
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37 Robertson, Rolls, Georges-Francois, & Panzeri, 1999; Taube, 1998). An analog system is
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39 assumed to exist in humans (Aguirre & D'Esposito, 1997; Sholl, Kenny, & DellaPorta, 2006).
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48 Other prominent examples for the computation of allocentric spatial representations are
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50 place cells and grid cells located in the hippocampal and entorhinal cortex (Hafting, Fyhn,
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52 Molden, Moser, & Moser, 2005; see Moser & Moser, 2008 for a review on both cell types and
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54 their function; O'Keefe & Dostrovsky, 1971). Together with head direction cells, the existence of
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3 these cell types indicates that computation of allocentric spatial representations is soft-wired and
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5 efficient allowing for building up allocentric representations upon first encounter with a new
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7 environment. Like egocentric reference frames, information embedded in allocentric reference
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9 frames plays a central role in higher order spatial cognitive processes like memory (Burgess,
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11 2006).

Development of the Neural Substrate for Reference Frame Computation

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Maturation of different structures of the human brain unfolds based on temporally distinct maturational trajectories (Gogtay et al., 2004). Lower-order sensorimotor regions have to be matured before higher-order association areas, integrating input from lower-order areas, follow in maturation. In addition, phylogenetically older structures mature earlier than phylogenetically newer areas. Brain areas associated with basic functions like motor control and sensory processing mature first, followed by areas involved in higher cognitive processing like spatial orientation. That is, maturation of the cortex is in agreement with regional relevant milestones in cognitive functioning (Gogtay, et al., 2004). Cortical structures underlying the computation of egocentric reference frames (e.g., the visual or vestibular cortex) mature prenatally to approximately 50% in primates. The visual cortical volume shows an overshooting growth pattern with a maximum at 8 postnatal months and a subsequent decline to adult levels. This development of cortical volume is paralleled by postnatal changes in neuropil volume and neuronal size, numbers of synapses, and dendritic spines (Garey, Michel, & Leuba, 1984; Huttenlocher & Decourten, 1987; Klekamp, Riedel, Harper, & Kretschmann, 1991). The same early developmental trajectory is present in cortical structures underlying the computation of allocentric reference frames like the hippocampus. The human hippocampus is approximately 40% mature at the time of birth. By 1 to 1.5 months it is 50% mature and reaches complete

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3 maturity by 15 months of age (Kretschmann, Kammradt, Krauthausen, Sauer, & Wingert, 1986).

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5 This is very early compared with the maturational timetable of the prefrontal cortex, which is
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7
8 thought to be fully mature around 10 years of age (Goldman-Rakic, 1987). It is also very early
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10 compared with the timetable of hippocampal maturation in the rat (Trice & Stanfield, 1986).

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12 With respect to dendritic growth and development of pyramidal neurons the maturation of the
13
14 human hippocampus seems to happen even earlier and faster than the visual cortex (Purpura,
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16
17 1975).

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20 The neural structures underlying the computation of egocentric and allocentric reference
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22 frames thus seem to be matured to a significant portion by the time of birth and proceed maturing
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24 along with developmental milestones of the human physical structure. Motor-milestones that are
25
26 important for the development of spatial cognitive processes include lifting and turning of the
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28 head at approximately 3 month, sitting upright around 6 months, and pointing and crawling
29
30 around 12 months postnatally. During this time overshooting growth patterns in cortical
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32 structures allow the infant to develop neural connections that support cognitive functions
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34 associated with the altered idiothetic inputs that might be necessary to trigger further maturation
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36 in cortical and subcortical structures like the hippocampus. The onset of crawling might be
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38 necessary for developmental changes in hippocampus and with that in allocentric coding of
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40 larger space. The development of motor programs is often associated with maturation of cortical
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42 structures connected to the developing area (Goldman-Rakic, 1987; Pine et al., 2002). Input from
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44 the vestibular and kinesthetic system might even be crucial for maintaining and further shaping
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46 of completely matured cortical structures underlying allocentric coding of space. One such
47
48 example is a severe hippocampal atrophy and impairment of allocentric spatial memory after
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50 vestibular loss (Brandt et al., 2005). In general, maturation of cortex and cognitive changes
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3 continue throughout late childhood and adolescence while adaptive changes of cortical structures
4 will proceed through a life-time(e.g., Gogtay, et al., 2004). Thus, motor development might be a
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6 necessary factor contributing to cognitive development but that does not imply that motor
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8 development is sufficient for the development of spatial cognitive abilities. This indicates that
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10 the fine pruning of neuronal connectivity in specific cortical structures is not the only
11
12 determining factor for an intact development of cognitive functions. Another important
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14 contributing factor might be the development of connectivity between cortical structures and
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16 adaptive changes due to the development or lesion of parts of cortical networks (Brandt, et al.,
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18 2005).

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25 Several key areas that are known to be involved in spatial cognitive processing reveal
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27 extensive interconnections. One central network in spatial navigation comprises among other
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29 areas the parietal, retrosplenial, and medio-temporal cortex (Byrne, Becker, & Burgess, 2007).
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31 While several other cortical areas are central for spatial orientation, e.g. the motor cortex and
32
33 frontal cortical areas, this network seems to comprise the ‘computational core’ to process and
34
35 store spatial information embedded in distinct reference frames. These areas are connected
36
37 through extensive bidirectional pathways, connecting the parietal and retrosplenial cortex
38
39 (Cavanna & Trimble, 2006), the retrosplenial and parahippocampal cortex, as well as
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41 retrosplenial cortex and movement related areas of the anterior cingulate cortex (Maguire, 2001;
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43 Vogt, Vogt, & Laureys, 2006). In addition, parts of the parietal cortex in primates project directly
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45 to the parahippocampus and subiculum while receiving afferences from the enthorhinal cortex
46
47 and layer CA1 in the hippocampus (Suzuki & Amaral, 1994). Further, multisensory parietal
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49 areas, the hippocampal formation, as well as the retrosplenial cortex are activated by vestibular
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51 stimulation (Vitte et al., 1996) indicating a direct influence of locomotion on activity in this
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3 network. These interconnections are sensitive to activity and thus will be pruned by their
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5 interactions or the absence of the same reflecting functional plasticity (Beckmann, Johansen-
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7 Berg, & Rushworth, 2009; Brandt, et al., 2005; Yu et al., 2011; Zhou et al., 2008).
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11 As a consequence of the functional connectivity, lesions to one or several parts of the
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13 network are usually associated with impairment in more than just one aspect of spatial cognitive
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15 processing. The impairment of a cortical structure that subserves a specific cognitive function,
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17 e.g. the computation of the navigator's heading, might be associated not only with impairments
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19 in the computation of heading but also with respect to the computation of other parameters that
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21 depend on the navigator's heading, e.g. the updating of egocentric bearing from other entities.
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23 Only detailed models with testable hypotheses based on physiological evidence can approach
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25 this general problem of first and higher order impairments. Aguirre and D'Esposito (1999)
26
27 describe one such theoretical framework on topographical disorientation based on an extensive
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29 literature research and earlier descriptions of the phenomenon (Farrell, 1996). Based on a review
30
31 of several case studies and their underlying lesion sites the authors identify 4 types of
32
33 topographical disorientation that are rooted in the egocentric and the allocentric domain. With
34
35 respect to the above described computational core network (parietal, retrosplenial, and
36
37 mediotemporal cortex), 'egocentric disorientation' is the only type of topographical
38
39 disorientation rooted in the egocentric domain. Egocentric disorientation is associated with
40
41 lesions in the superior parietal cortex. Patients with lesions in this area display severe difficulties
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43 in understanding and using the spatial relationships of object with respect to their own position
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45 and orientation (Aguirre & D'Esposito, 1999; Wilson et al., 2005). Other examples of pure
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47 egocentric disorientation are associated with lesions in inferior parietal cortex which might serve
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49 the computation of an egocentric reference frame for spatial exploration (Karnath, 1997). The
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3 complex integration of different reference frames in parietal cortex (Andersen & Buneo, 2002;
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5 Andersen, et al., 1997) are fundamental to general spatial orientation abilities and thus lesions to
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7 the superior or inferior parietal cortex are usually associated with more than pure egocentric
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9 disorientation dependent on the size of the lesion (e.g., Seubert, et al., 2008).
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13 Further types of topographical disorientation are rooted in the allocentric domain. The
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15 first type of allocentric disorientation, 'heading disorientation', is associated with an inability to
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17 derive directional information from prominent landmarks that are recognized by the patient
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19 (Aguirre & D'Esposito, 1999; Takahashi, Kawamura, Shiota, Kasahata, & Hirayama, 1997). The
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21 lesions underlying this type of disorientation are restricted to the retrosplenial cortex (Maeshima
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23 et al., 2001; Maguire, 2001; Takahashi, et al., 1997). Recent studies suggest that lesions to the
24
25 retrosplenium are also associated with the inability to update object locations with changes in the
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27 orientation of the observer, indicating a role of the retrosplenial cortex for the conversion of
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29 egocentric and allocentric information (Hashimoto, Tanaka, & Nakano, 2010). The other two
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31 types of allocentric disorientation are 'landmarks agnosia' describing the inability to use salient
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33 features of the environment for orientation and 'anterograde amnesia' describing the inability to
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35 orient in new environments while orientation in familiar environments is preserved (Aguirre &
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37 D'Esposito, 1999; Takahashi & Kawamura, 2002). Both of the two latter types of disorientation
38
39 are associated with lesions in or near the occipito-temporal junction and the parahippocampus.
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41 Recently a new form of topographical disorientation, i.e. 'developmental topographical
42
43 disorientation' (DTD) was described by Iaria and colleagues (Bianchini et al., 2010; Iaria &
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45 Barton, 2010; Iaria, Bogod, Fox, & Barton, 2009). The condition describes the inability of
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47 patients to orient within the environment without revealing cortical lesions. Patients with DTD
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49 demonstrate a specific deficit in computing and maintaining a cognitive map of the environment
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EMBODIMENT OF SPATIAL REFERENCE FRAMES

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3 (Iaria & Barton, 2010; Iaria, et al., 2009). Since this is a newly discovered condition and sample
4 sizes are fairly small, results have to be considered with cautious. However, if future studies can
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6 clarify contributing factors and discover further evidence for potential genetic aspects of DTD
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8 this condition might shed new light on the interaction of spatial cognitive processes and their
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10 neural substrate during human orientation.
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15 In summary, the functions of spatial cognitive processing are located in cortical regions
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17 that are strikingly similar in different species indicative of an evolutionary old system central to
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19 the survival of a species. The neural basis for these cortical regions is genetically determined
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21 resulting in soft-wired neural structures that adapt to cognitive activity. The cortical areas of the
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23 ‘core computational’ spatial network proposed here are heavily interconnected and build the
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25 basis for the computation and maintenance of spatial information based on distinct reference
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27 frames. Small and circumscribed lesions can be associated with very specific impairments in
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29 spatial cognitive processing but more likely lesions are more wide-spread and thus affect more
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31 than one aspect of spatial disorientation.
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Individual Proclivities And Cortical Plasticity

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41 Whenever a navigator moves in his or her environment a multitude of sensory
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43 information is processed automatically based on both egocentric and allocentric reference
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45 frames. This is possible because of the soft-wiring and efficient computation of information
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47 based on egocentric and allocentric reference frames in the human brain. Changes in the physical
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49 structure of the navigator are associated with changing motor behaviors allowing for the
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51 development of neural structures and connections between cortical areas underlying the
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53 computation, maintenance, and transfer of information based on distinct reference frames. But
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3 what are the sources of individual differences in spatial navigation?
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6 Besides individual differences in the maturation of neural structures underlying spatial
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8 cognitive processes a multitude of additional factors will influence the development of individual
9
10 spatial strategies. Attributes of and experience with an environment (Aporta, 2002), age
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12 (Newcombe & Huttenlocher, 2003), as well as biological factors (Lovden et al., 2010) will
13
14 contribute to a preference for selecting a specific subset of reference frames during navigation.
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16 The dominant use of a specific reference frame over the course of an individuals' development is
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18 accompanied by structural changes in the associated neural networks.
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22 The socio-cultural environment shapes the way navigators reason about and use symbols
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24 and language to represent and communicate space. Languages differ in the predominant
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26 linguistic frame of reference used for expressing spatial relations (Haun, Rapold, Janzen, &
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28 Levinson, 2011; Levinson, 1996; Majid, Bowerman, Kita, Haun, & Levinson, 2004). Some
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30 languages miss concepts that correspond to the egocentric description of object relations like
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32 "left", "right", or "front", "back" (e.g., the Australian language Guugu Yimithirr; see Levinson,
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34 2003). This however, does not imply the absence of egocentric concepts in these languages.
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36 Reference frame-specific spatial concepts as communicated through language will shape the way
37
38 an individual cognizes and communicates about space (Haun, et al., 2011) and thus, will
39
40 contribute to shaping the underlying neural networks. Another environmental factor contributing
41
42 to reference frame proclivities is the geographical region a navigator lives in, how long he or she
43
44 is exposed to an environment, and how he or she interacts with that environment. The specifics
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46 of a geographical environment like those of developed areas (e.g., New York City) as compared
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48 to Tundra areas (e.g., Arctic Tundra) influence the way navigators represent their surroundings.
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50 Navigators might experience difficulties in perceiving and using distal landmarks in a dense
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3 urban environment like New York City. That, however, does not imply the absence of allocentric
4 spatial representations in navigators in such an environment. Nor does it imply a preference for a
5 specific reference frame in people living in that area. Individual differences exist between
6 cultures and residential environments just as they exist within cultures and residential
7 environments. However, wide-open areas like the Arctic Tundra or the sea ice of the Arctic
8 Archipelago might foster the use of distal landmarks (or icemarks in case of the Archipelago)
9 integrated in an allocentric reference frame to guide navigation (Aporta, 2002, 2005; Istomin &
10 Dwyer, 2009).

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22 Living in a specific geographical environment, embedded in a certain culture, the
23 navigator learns to use one or another reference frame (or a subset of reference frames) to reach
24 navigational goals. As long as the selected reference frame is successful in solving the navigation
25 task there is no need to use a different reference frame (or combination of a subset thereof). In
26 some navigators one strategy, i.e. the use of one reference frame or a combination of a subset of
27 reference frames might be sufficient for most of the navigational tasks encountered during the
28 first years of life. The more a specific reference frame is used, the stronger the neural
29 connections become that underlie the computation of that reference frame. Over time, the
30 cortical structures that are associated with the computation of the preferred reference frame will
31 likely show increased gray matter (reflecting more neurons an/or neuronal connectivity) as
32 compared to the neural structures associated with the computation of the non-preferred reference
33 frame.
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51 This assumption is supported by recent neuroimaging studies revealing structural changes
52 accompanying the use of specific reference frames to solve spatial tasks. While the preferred use
53 of an allocentric reference frame is associated with increased gray matter in the hippocampus and
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3 adjacent structures the use of an egocentric reference frames is associated with increased gray
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5 matter in the caudate nucleus (Bohbot, Iaria, & Petrides, 2004; Bohbot, Lerch, Thorndyraft,
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7 Iaria, & Zijdenbos, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire, Frackowiak,
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9 & Frith, 1997; Maguire et al., 2000). One interesting aspect of this seems to be a form of
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11 competition between structures responsible for the computation of distinct reference frames.
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13 Increased gray matter in the hippocampus (allocentric reference frame) seems to be correlated
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15 with reduced gray matter in the caudate nucleus (egocentric reference frame) and vice versa
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17 (Bohbot, et al., 2007; Iaria, Chen, Guariglia, Ptito, & Petrides, 2007). Finally, use of egocentric
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19 and allocentric reference frames in a flexible manner is associated with comparable gray matter
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21 volumes in both, the hippocampus and the caudate nucleus. If a navigator learns to use distinct
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23 reference frames dependent on the spatial environment, the situation and so forth, the neural
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25 structures underlying different reference frames will be developed to comparable levels.
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32 In summarizing, the neural structures that allow for efficient computation of distinct
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34 egocentric and allocentric reference frames are genetically predetermined. These cortical
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36 structures demonstrate vulnerable periods that seem central for maturation but will develop over
37
38 the time course of an individual lifespan. Specific programs, like the development of crawling
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40 might be necessary for the maturation of cortical structures underlying reference frame
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42 computation. However, additional factors like the socio-geographical environment and
43
44 personality will contribute to a selective maturation of reference frame-specific cortical
45
46 structures. As a result, all navigators are able to compute and maintain an egocentric and
47
48 allocentric representation of their surroundings, even when a specific environment is first
49
50 encountered. But individual differences that result from cortical maturation and learning will
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52 lead to a proclivity to use one or the other reference frame. The knowledge of such individual
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3 differences is of importance for understanding human spatial behavior in disciplines like
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5 psychology, geography, and the neurosciences.
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To Turn Or Not To Turn: Brain Imaging of Embodied Spatial Cognition

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12 Numerous questionnaires, map designs, and brain imaging studies analyzed individual
13 spatial cognitive abilities. Only a minority of these considered individual differences in the
14 preferred use of distinct reference frames. This is especially intriguing for imaging studies that
15 map the cortical networks underlying spatial cognitive tasks in virtual reality (VR). Nonetheless,
16 a large number of neuroimaging studies using virtual reality environments proposed to have
17 identified a distributed network of brain regions accompanying the use of distinct reference
18 frames during spatial orienting. According to those studies, human navigation in VR is
19 associated with activity in a network comprising the hippocampus, parahippocampus, caudate
20 nucleus, parietal and retrosplenial cortices, and regions within prefrontal cortex (PFC) (Aguirre
21 & D'Esposito, 1997; Ekstrom et al., 2003; Gron, Wunderlich, Spitzer, Tomczak, & Riepe, 2000;
22 Hartley, Maguire, Spiers, & Burgess, 2003; Maguire et al., 1998; Maguire et al., 2003; Shelton &
23 Gabrieli, 2002; Voermans et al., 2004; Wolbers & Buchel, 2005). The results suggest that the use
24 of an allocentric reference frame is associated with activity in a network comprising the
25 hippocampus, amygdala, as well as the parahippocampal, perhinal, entorhinal, and orbitofrontal
26 cortices (Bohbot, et al., 2007; Iaria, et al., 2003). Allocentrically coded information is stored in
27 hippocampus with place cells and grid cells providing input to the cognitive map and path
28 integration system (Doeller, Barry, & Burgess, 2010; Doeller, King, & Burgess, 2008; Ekstrom
29 et al., 2005; Ekstrom, et al., 2003; Kahana, Sekuler, Caplan, Kirschen, & Madsen, 1999;
30 Whitlock, Sutherland, Witter, Moser, & Moser, 2008). The use of an egocentric reference frame,
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3 in contrast is associated with increased activity in the caudate nucleus, posterior parietal cortex,
4 as well as the human motion complex (Andersen & Buneo, 2002; Etchamendy & Bohbot, 2007;
5 Iaria, et al., 2003; Whitlock, et al., 2008; Wolbers, Weiller, & Buchel, 2004; Wolbers, Wiener,
6 Mallot, & Buchel, 2007). The integration of spatial information based on distinct reference
7 frames and located within different cortical structures is assumed to depend on the retrosplenial
8 and posterior parietal cortices (Andersen & Buneo, 2002; Byrne, et al., 2007; Maguire, 2001;
9 Whitlock, et al., 2008). The posterior parietal cortex integrates information based on different
10 reference frames supporting different actions and thus allows a tight coupling of spatial coding
11 with action through its strong connection to motor and premotor cortices (Andersen & Buneo,
12 2002; Goodale & Milner, 1992).

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27 Most of these studies required participants to sit still or lie prone to avoid movement-
28 related artifacts from distorting the signal of interest (Makeig, Gramann, Jung, Sejnowski, &
29 Poizner, 2009). The absence of any natural movement, however poses a serious problem for the
30 navigator. Idiothetic information that is needed to update egocentric and allocentric spatial
31 representations is missing. In other words, an embodied process of spatial orientation in the
32 natural world becomes dis-embodied in the virtual world. In the presence of natural sensory
33 information, i.e., when visual, vestibular, and kinesthetic information can be combined
34 computation of egocentric spatial representations is efficient. Even more, any attempt to ignore
35 sensory information on body rotation reveals errors and effortful cognitive processing to re-
36 compute automatically updated heading changes (Farrell & Robertson, 1998). In VR
37 environments, in contrast, when participants lack sensory feedback on heading changes, a
38 decline in spatial orienting is observed (Chance, Gaunet, Beall, & Loomis, 1998; Israel &
39 Warren, 2005; Klatzky, et al., 1998). Participants are able to update their position and orientation
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3 relative to landmarks that they have learned under real movement conditions but fail to do so for
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5 imagined movement (Klatzky, 1998; Rieser, Guth, & Hill, 1986; Sholl, 1989). Even though
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7 participants are able to respond in accordance with imagined heading changes, reactions are
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9 significantly slower and less accurate as compared to physical rotations (Easton & Sholl, 1995;
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11 May, 1996; Presson & Montello, 1994). It seems that when participants imagine heading changes
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13 and miss vestibular and kinesthetic feedback, they fail to update spatial representations. This is at
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15 least true for a subgroup of the populations under study (Gramann, et al., 2005; Gramann, et al.,
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17 2010; Riecke, 2008; Riecke, van Veen, & Bulthoff, 2002).

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22 These findings demonstrate the artificiality of virtual orientation experiments that require
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24 the navigator to resort to strategies that compensate for the absence of natural idiothetic
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26 information. While these approaches fail in specifying spatial cognitive processes that occur
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28 under natural conditions, they are nonetheless informative with respect to the limits of spatial
29
30 cognitive processes and the general cognitive architecture underlying human spatial navigation.
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32 One example is the tunnel task, a passive VR path integration task to investigate spatial orienting
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34 processes and their underlying brain dynamics (Gramann, et al., 2005; Schönebeck, Thanhäuser,
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36 & Debus, 2001). In this task participants have to keep up orientation while traversing virtual
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38 tunnels with one or more turns to the left or right. At the end of each passage they have to adjust a
39
40 homing vector indicating the origin of their travel. Even though the visual flow stimulation is
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42 identical for all participants half of the participants use an egocentric reference frame while the
43
44 other half of the participants uses an allocentric reference frame to point back to the origin (see
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46 Figure 1). Figure 1 displays an exemplary subject using an allocentric reference frame as dark
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48 grey head. This navigator perceives heading changes during a stimulus turn to the right but
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50 chooses to react based on a cognitive heading that does not incorporate the perceived heading
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3 changes (as if the navigator at the end of the passage had the same heading as in the beginning of
4 the passage). Participants using an allocentric reference frame were labeled 'Nonturner' while
5 participants using an egocentric reference frame are labeled 'Turner' (Gramann et al., 2005).

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8 This strategy group, displayed as light grey head, updates the cognitive heading according to the
9 perceived heading changes during a stimulus turn. After a passage with a turn to the right
10 Nonturners would point back to their left to indicate the starting position while Turner would
11 point back to their right to indicate the origin of the identical tunnel passage.
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20 These studies demonstrate that identical visual flow information in a disembodied spatial
21 VR task (in the sense that no according vestibular and kinesthetic information is given) is
22 associated with different cognitive strategies to solve the task. Using only sparse visual flow
23 subjects are able to solve the task based on their preferred reference frame without differences in
24 their eye movements and thus no differences in what information is used for building and
25 maintaining a spatial representation (Gramann, El Sharkawy, & Deubel, 2009). Even when
26 instructed to use their non-preferred reference frame subjects demonstrate no decline in homing
27 accuracy which is indicative of a parallel computation and maintenance of distinct reference
28 frames (Gramann, et al., 2005). Further support for the parallel computation and maintenance of
29 distinct reference frames comes from the cortical activity patterns accompanying the use of
30 different reference frames (Gramann, et al., 2006; Gramann, et al., 2010; Plank, Müller, Onton,
31 Makeig, & Gramann, 2010). These results indicate that more than one frame of reference is
32 active at all times but that only one preferred reference frame is used to solve the task (Gramann,
33 et al., 2010). Results from imaging studies demonstrate a preference to use a certain reference
34 frame in most of the participants but also that some participants can change orienting strategies
35 over the time course of an experiment (Bohbot, et al., 2007; Etchamendy & Bohbot, 2007; Iaria,
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3 et al., 2003).

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5 It can be concluded that an efficient and most accurate spatial orienting in complex
6 environments takes place only when the navigator is able to perceive information from all
7 relevant senses. This is the case when participants are free to move in their environment.
8
9 Investigations trying to image the brain dynamics underlying spatial cognition force subjects to
10 sit still or lie prone while orienting because traditional imaging methods use sensors that are too
11 heavy to follow the navigator's movement (e.g., functional magnetic resonance imaging, fMRI;
12 Magnetencephalography, MEG) and the analyses approaches used in traditional brain imaging
13 consider movements (even eye movements) as primary source of artifacts in the recorded data
14 (Makeig, et al., 2009). Increasing evidence of individual differences in spatial cognitive abilities
15 and evidence for the artificiality of spatial cognitive processes that dis-embodify the participant
16 show the need to use different approaches to this increasingly important topic. The development
17 of new theoretical frameworks has to incorporate a *paripassu* view regarding the relevance, use,
18 and interaction of spatial reference frames. Finally, attempts to image the brain dynamics
19 underlying embodied spatial cognition need to use mobile methods that allow for investigating
20 the functional coupling of the brain and the body to gain new insights into the cognitive
21 architecture of natural and embodied spatial orientation (Gramann, Gwin, Bigdely-Shamlo,
22 Ferris, & Makeig, 2010; Gwin, Gramann, Makeig, & Ferris, 2010, 2011).
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Figure Captions

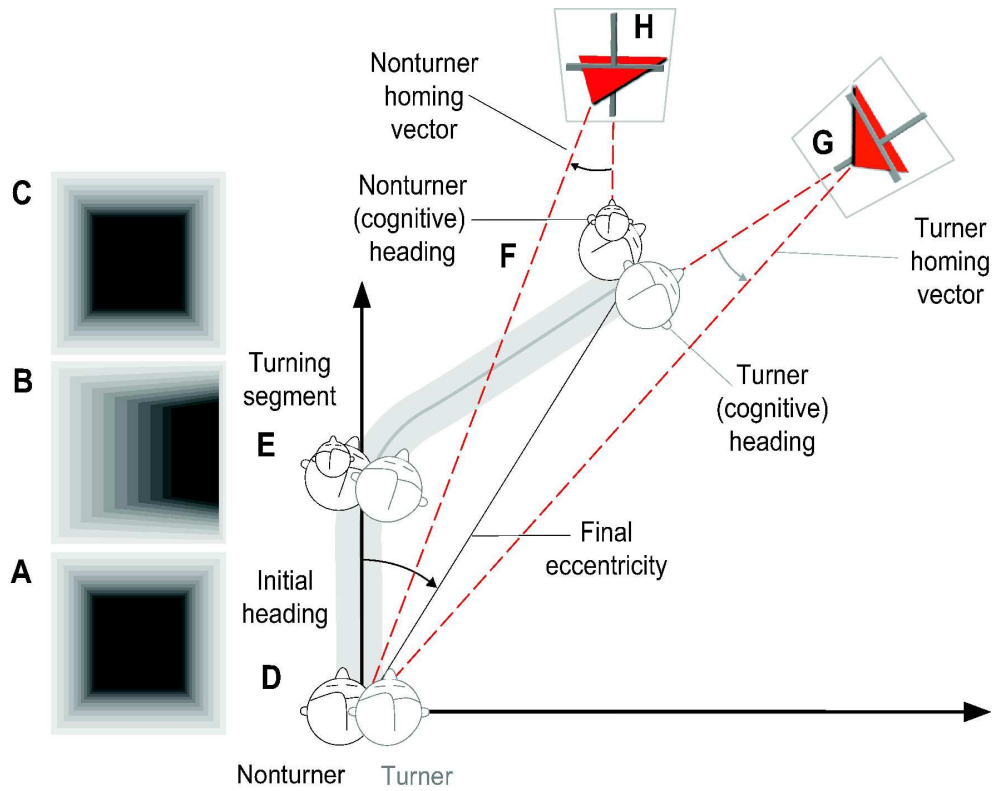
Figure 1: Left panel displays a schematic depiction of a tunnel passage with (A) a first straight segment, (B) a second turning segment with a turn to the right, (C) a third straight segment. The right panel displays an aerial view on the tunnel passage with (D) dark gray head depicting a Nonturner and a light gray head depicting a Turner subject at the beginning of the tunnel passage, (E) during the stimulus turn, and (F) at the end of the tunnel passage. In (G) and (H) the correct homing vectors are displayed for Turners and Nonturners, respectively.

Footnotes

Footnote 1: Please note that the terms ‘straight ahead’ and ‘turn left’ are defined in an egocentric reference frame referring to the momentary heading (the etymology of ‘ahead’ is ‘at the head, in front’) of the navigator when the train station is behind him/her.

Footnote 2: *Ontogenesis* describes the origin and development of an organism from the fertilized egg to its mature form. Here it is used to describe the maturation of the individual with respect to spatial knowledge. *Microgenesis* describes the development of an individual organism caused by the process of acquisition (of learning, imitation, etc.) in time periods that vary from moments to longer periods of times (e.g., months).

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Left panel displays a schematic depiction of a tunnel passage with (A) a first straight segment, (B) a second turning segment with a turn to the right, (C) a third straight segment. The right panel displays an aerial view on the tunnel passage with (D) dark grey head depicting a Nonturner and a light grey head depicting a Turner subject at the beginning at of the tunnel passage, (E) during the stimulus turn, and (F) at the end of the tunnel passage. In (G) and (H) the correct homing vectors are displayed for Turners and Nonturners, respectively.

227x181mm (600 x 600 DPI)

Only