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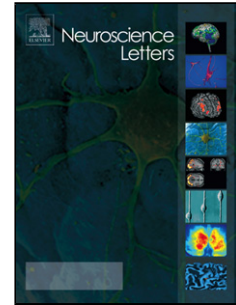


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Don't get lost in translation: the role of egocentric heading in spatial orientation

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Highlights

- Our data showed that a small scale map facilitated spatial retrieval.
- This suggested the primary role of egocentric heading information for orientation.
- Our data are consistent with the role of retrosplenial cortex in spatial translation.

Abstract

Much is known about how different spatial reference frames continually interact to support spatial navigation, but less explored is whether it is more crucial to process object-to-object information or egocentric heading information for effective orientation in a cluttered environment. To address this question, we evaluated the possible influence on spatial performance of an interactive aerial view of different scale (small vs. large) comprising an arrow indicating participants' egocentric heading. Results revealed that the presence of a small interactive aerial view including a visualized larger arrow facilitated the retrieval of stored spatial layout. These data are consistent with recent studies revealing the role of retrosplenial cortex in translating between different spatial reference frames, and may contribute to elucidate the continuous synchronization between the inter-object direction information in the environment with respect to egocentric current heading.

Keywords: Spatial Orientation, Spatial Reference Frames, Retrosplenial Cortex, Virtual Reality

Introduction

The ability to navigate in our surrounding environment is a vital behavior, necessary to track a route from one place to another [1]: in this manner, individuals are able to remember an important spatial location (i.e., “How can I remember where I left my car?”), other locations (i.e., “My car was near the red car”), as well as its relation to themselves (i.e., “The red car was at my left when I entered in the supermarket!”). First, it implies the capacity to represent the relations

between the objects in space (i.e., *allocentric reference frame*), and between these objects and ourselves (i.e., *egocentric reference frame*) [2]. The allocentric reference frame is constituted by object-to-object relationships, and spatial information is represented with respect to external elements for an extended period of time, specifically in the hippocampal area [3-5]. Conversely, the egocentric reference frame, which is constituted by self-to-object relationships, maintains and updates spatial information in relation to the current individual's position and heading with respect to the surrounding environment, especially in the posterior parietal area [6-10]. Much is known about how these different spatial reference frames continually interact to support spatial navigation [11-13], but it is still less explored how it is possible to anchor our current egocentric heading in the environment for an effective orientation.

According to recent neuroscientific evidence, a crucial role was assigned to the retrosplenial cortex (RSC), which is responsible for the continuous transformation between the spatial reference frames [14, 15]. Already Aguirre and D'Esposito [16] have introduced "heading disorientation" in their taxonomy of topographical disorientation, specifying that after a damage in RSC, patients may present a difficulty in updating direction of orientation with respect to the external relevant stimuli. In this direction, Takahashi and colleagues [17] reported three patients with right retrosplenial lesion who were able to identify familiar objects, but showed a great impairment in remembering directional orientation between two locations. Indeed, for an effective orienteering, when we memorize the relationships between objects in space, we also encode the inter-object direction in respect to our current egocentric heading, resulting in an "ego-oriented bearing" from one object to the other [18]. Marchette and colleagues [19] clarified the role of RSC in establishing one's position and heading relative to external elements of our space. Using fMRI, they found that RSC is responsible for anchoring spatial reference frames to

local environmental features, that may be generalized across local environments with similar geometrical structure. These findings showed that the retrieval of information is constrained by a specific reference to the observer's body (i.e., the egocentric current heading): it means that there is an alignment principle for anchoring the local environmental features with the previous stored one. Serino and Riva [20] found that participants were more precise in retrieving the position of an object when immersed in an egocentric experience with an interactive aerial view of the experienced virtual environment, since it provides information about their heading in the space. These preliminary findings are in value in supporting the role of the so-called mental frame syncing in the spatial processing [21, 22], namely a cognitive process that permits an effective retrieval by the synchronization of the two types of allocentric representations [23], the viewpoint-independent representation (i.e., including object-to-object information) and the allocentric viewpoint-dependent representation (i.e., including information about egocentric current heading). Some evidence has shown that two regions within the hippocampus are specifically involved in the processing of allocentric information [24, 25]. One is region CA3, which receives inputs from the entorhinal cortex and encodes an allocentric representation of the spatial scene toward which the individual orients. This is what Behrendt calls the allocentric viewpoint-dependent representation [23]. The second region consists of the neurons in CA1, which receives inputs from CA3 via Schaffer's collaterals and encodes allocentric representations involving only abstract, object-to-object information. This is what Behrendt calls allocentric viewpoint-independent representation [23].

On these premises, the main objective of the current study is to understand whether it is more crucial the role of object-to-object information or egocentric heading information for an effective spatial orientation. To achieve this aim, we evaluated the possible influence on

performance of interactive aerial views of different scale (small vs. large) comprising arrows indicating participants' egocentric heading.

Spatial layouts were encoded and retrieved in a Virtual Reality (VR) immersive setup, and specifically in a computer-assisted virtual environment (CAVE). VR has already been confirmed to be a suitable medium to study complex spatial processing, since it gives the possibility to manipulate the perspective when investigating individuals' ability to reorient in space [26, 27]. Moreover, in a CAVE, visual images are back-projected onto the screen of a small room surrounding the users, whose movements are tracked by sensors and the projections are adjusted continually to retain the users' viewpoints. Thanks to these features, it is possible to investigate how the interactive aerial view, and its arrow, rotates according to the direction of the participants' current egocentric heading direction.

Material and Methods

Thirty participants [15 females and 15 males, mean age: 29.03 (8.90)] from the Institute of Movement Sciences Etienne-Jules Marey (Marseilles, France) took part in the study. All of the participants signed an informed consent form prior to participation. First, stereoscopic acuity was assessed to exclude participants with severe vision disorders. Then, the interpupillary distance (i.e., the distance between the pupils) was measured for each participant to calibrate the projection and to avoid possible feelings of discomfort (for example, nausea or headache) due to a conflict between visual and vestibular signals that may occur when navigating in an immersive virtual environment. After initial training in VR technology and the navigation interface (i.e., a simple navigation task in a large environment), the experimental procedure was initiated,

consisting of an encoding phase, which was followed by the retrieval phase in three different conditions. The participants were placed in the centre of the CAVE, consisting of four projection screens: frontal, ground and lateral projections. Each frontal and lateral screen had a projection surface of 3 meters wide by 4 meters high. The three vertical walls were back-projected and the ground received direct projection with a 1400x1050 resolution and a 60 Hz frame rate.

Stereoscopic projection was obtained by two digital light processing projectors attached to each projection surface. A motion capture system (ArtTrack), based on a set of eight cameras, allowed tracking the position and orientation of the observer's head in the environment and constantly updated the stereoscopic projected images according to the subject's point of view. The participants also had a Flystick (ArtTrack), a wireless interaction device that allowed them to explore and to interact with the environment by using a joystick on the top.

A virtual city (125 meters by 150) was developed as the test environment. It was built around a central square with a tower in the middle, which represents the starting point of the navigation. In the encoding phase, starting from the center, each participant was instructed to find and memorize the position of a hidden plant with no time limit. The first group of participants searched for the hidden object while navigating in the virtual city without any interactive aerial view of the city (i.e., "encoding without an interactive aerial view"). A second group of participants could see a small scale aerial view of the virtual city that was always available in the field of view (i.e., "encoding with a small scale interactive aerial view"). Finally, a third group of participants could see a large scale interactive aerial view of the virtual city, always available in the field of view (i.e., "encoding with a large scale interactive aerial view"). Both "maps" (and their arrows) had the same size, but different scales: the first one had a visible radius of 25 meters (i.e., small scale), and consequently, a visualized larger arrow indicating the

current egocentric heading of participants. The second map, instead, had a visible radius of 50 meters (i.e., large scale), and consequently a visualized smaller arrow. See Figure 1 for an overview of the virtual city with the three experimental manipulations used for encoding and retrieval.

[Insert Figure 1]

In the retrieval phase, all participants were asked to retrieve the position of the hidden plant in three different conditions (i.e., "retrieval without the interactive aerial view", "retrieval with a small scale interactive aerial view" and "retrieval with a large scale interactive aerial view"), entered in the virtual city from another starting point. To indicate the position of the object in the virtual city environment, this technique forced the participants to refer to their allocentric viewpoint-independent representation and sync it with the allocentric viewpoint-dependent representation [28]. Specifically, it forced participants to place their current egocentric heading to indicate the objects' bearings in the surrounding environments. When this new "ego-oriented bearing" [18] is the same as the one memorized, an effective retrieval can be achieved. The order of the conditions was randomized for each participant with no time limit. In the condition "retrieval without the interactive aerial view" participants entered the virtual city from the North, and attempted to retrieve the position of the plant they had discovered in the encoding phase. In the second condition – "retrieval with a small scale interactive aerial view" - starting from the South, participants were able to visualize the virtual city on a small scale interactive aerial view during the navigation. In the last condition – "retrieval with a large scale interactive aerial view" – the task was the same, but they had a large scale interactive aerial view of the virtual city available during navigation, and they started from the West. In all three conditions, they were instructed to stop and tell the experimenter when they were sure they had reached the

correct position (i.e., the plant was absent). As previously explained (see Figure 1), also for the retrieval phase both “maps” (and their arrows) had the same size, but different scales and consequently different visualized arrows. The experimental design has been summarized in Figure 2.

[Insert Figure 2 here]

Path accuracy (i.e., a measure of an effective spatial retrieval) in the three conditions is the dependent variable. Differences in the path accuracy were calculated using a repeated measure analysis of variance with Retrieval the within factor and Encoding as the between factor. Path accuracy was computed by calculating the total length of the path traversed in each retrieval condition, then dividing by a reference path calculated through a computer simulation. Indeed, the result of this ratio expresses the percentage of accuracy with respect to this “reference path”, where values over 100% represent the multiplier rate relative to the reference path; e.g. 120% is 20% longer than the necessary path (i.e., participants showed some difficulties in remembering the path), and 80% is 20% shorter than the reference path (i.e., participants had no difficulties in remembering the path, since they performed better than the path used as reference). The Greenhouse-Geisser test statistic was used when the assumption of sphericity was violated. Pairwise comparisons (with Bonferroni’s adjustment) were computed to compare significant differences. Finally, for all analyses, determination of significance was based on $\alpha = 0.05$.

3. Results

Data were entered into Microsoft Excel and analysed using SPSS version 18 (Statistical Package for the Social Sciences–SPSS for Windows, Chicago, IL, USA).

A repeated measure analysis of variance was conducted to investigate the differences in the path accuracy with Retrieval (“retrieval without the interactive aerial view” vs. “retrieval with a small scale interactive aerial view” vs. “retrieval with a large scale interactive aerial view”) as the within factor and Encoding (“encoding without the interactive aerial view” vs. “encoding with a small scale interactive aerial view” vs. “encoding with a large scale interactive aerial view”) as the between factor. One participant was excluded from the analysis because of problem in data recording.

First, no significant effect of Encoding was found, i.e. the presence of the interactive aerial view (small and/or large scale) during the encoding phase had no influence on the path accuracy. This means that there was no effect of the presence of a viewpoint-dependent representation in facilitating the retrieval of the memorized spatial layout for an effective navigation. On the other hand, the main effect of Retrieval [$F(2, 52) = 8.664$ $p < 0.01$, $\eta^2 = .250$] was significant. Pairwise comparisons (Bonferroni's adjustment) indicated that the performance in the retrieval condition with the small scale interactive aerial view was significantly better ($M = 93.54$; $SD = 3.31$ $p < .01$) when compared to the performance in the retrieval condition without the interactive aerial view ($M = 113.80$; $SD = 5.18$) and to the performance in the retrieval condition with the large scale interactive aerial view ($M = 106.87$; $SD = 4.31$).

As shown in Figure 3, participants were significantly more accurate in remembering the path (reproducing a path 6.5% shorter than the reference path) when they were able to visualize the small scale interactive aerial view, which included a visualized larger arrow oriented according to their egocentric heading in the virtual scene.

[Insert Figure 3 here]

4. Discussion

Driven by recent neuroscientific findings emphasizing the role of an alignment principle centred on the observer's body that may guide continuous transformation between the egocentric and allocentric reference frames, the main objective of this study was to understand whether it is more crucial the role of object-to-object information or egocentric heading information for an effective spatial orientation. An interactive aerial view during navigation was supposed to give additional information about object-object information, while its arrow, oriented according to the direction of the participants' heading, is supposed to give additional information about egocentric direction in the world.

Some studies have already investigated the influence of maps as navigational aids on performance, with contrasting results. For example, Darken and Sibert [29] found that the use of a map improved the performance of users performing a complex searching tasks in a number of virtual worlds. However, some researchers have pointed out that the use of a map may negatively affect spatial behavior since it forced a continuous change from an egocentric perspective to an allocentric one [30, 31].

Our findings revealed that participants were significantly more accurate in remembering the correct path when they had a small scale "map" of the environment. First, these results showed that the presence of any kind of additional information during the encoding phase is useless for a functional organization of spatial knowledge. On the other side, the presence of a of a small scale interactive aerial view facilitated the retrieval of stored spatial layout. In fact, as previously explained, the small scale interactive aerial view included an arrow, which appeared as "larger" in comparison to that in the large scale interactive aerial view because of the scale of

visualization. Probably, the presence of a larger visualized arrow giving more comprehensive information about the current egocentric heading in the environment was effective in supporting the navigation. Moreover, the large scale interactive aerial view (and its visualized smaller arrow) did not provide additional help to the participants' performance: apparently, it is not a problem of the "quantity" of object-to-object information, but it might be more related to the cognitive synchronization between the allocentric viewpoint-independent representation (including also object-to-object information) and the allocentric viewpoint-dependent representation (i.e. comprising information about the current egocentric heading in the environment), as suggested by the "mental frame syncing hypothesis" [21, 22].

Indeed, it was shown that when we orient ourselves in an environment, we to have to re-establish our ego-oriented bearing [18] on a pure allocentric map by mentally computing the bearing of each relevant "object" in relation to our current heading in space. In sum, a visualized larger arrow, which indicated clearer our current heading direction in relation to objects, appears to be more useful than a large scale map in facilitating the retrieval of stored spatial layout.

Taken together, these findings may contribute to elucidate the role of RCS in translation between different reference frames. A recent study on the rat dysgranular RCS may raise the question of whether the RSC may also be involved in another mechanism needed to navigate, namely the integration of sensorial information from multiple modalities [32]. However, although fMRI studies would be crucial to support the role of RCS in the cognitive synchronization between the allocentric viewpoint-independent representation with the allocentric viewpoint-dependent representation [20-22], our data preliminarily emphasized the primary importance of the egocentric current heading information for spatial orientation. This evidence suggest that, coherently with its interconnectivity with the hippocampus, the RCS may

selectively engaged in translating the stored allocentric reference frame to an egocentric one thanks to a re-establishment of an “ego-oriented bearing” [18], resulting from the continuous synchronization between the inter-object direction in the environment in respect to egocentric current heading. A recent study carried out by Julian and colleagues gave support to our findings [33]. They examined the navigational behavior of mice in two tasks, in which animals had to recognize the chamber in which they were located (i.e., place recognition) and to retrieve their facing direction within that chamber (i.e., heading retrieval). Their results demonstrated that nongeometric features are crucial for place recognition. On the other side, showing the dissociability between these two spatial cognitive processes, mice failed to use the same features for heading retrieval, relying only on the geometric shape of the chamber.

Recent advancement in VR technology offers the chance to further investigate the existence of separate cognitive systems for place recognition and heading retrieval, thanks to the integration of head-mounted eye tracking systems in a CAVE. The benefit of analyzing eye movement data is the possibility to investigate where participants direct their visual attention for place recognition, and then how they synchronize their current heading to successfully accomplish a path retrieval task. As another future challenge, this would permit also to explore individual differences in the ability in the mental frame syncing [20-22]. Since our data showed that participants who were immersed in a virtual environment benefited from a small interactive aerial view, it would be interesting to investigate how "spatial visualizers" (namely, individuals who tend to use imagery to represent and transform spatial relationships [34-36]) transform additional spatial information from this interactive aerial view and use it to better synchronize their egocentric heading in relation to salient landmarks.

Competing interests

The authors declare that they have no conflict of interests.

Authors Contributions

S. Serino wrote the first draft of the manuscript. G. Riva, D. Mestre, P. Mallet, J. M. Pergandi and P. Ciproso were involved in a critical revision of the manuscript for important intellectual content. All the authors approved the final version of the manuscript for submission.

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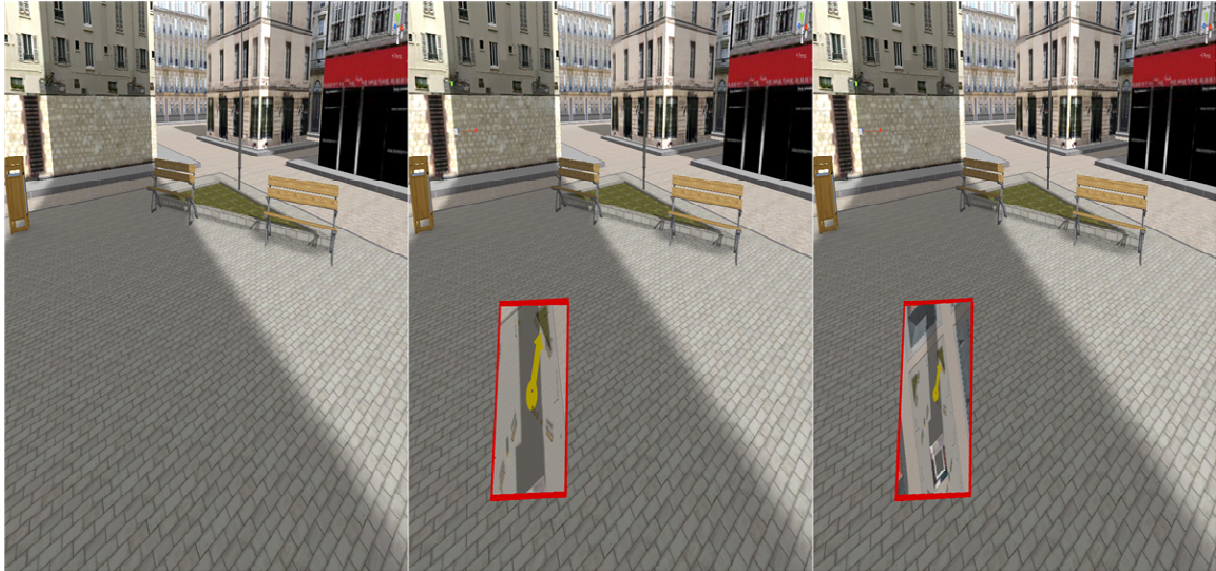
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Figure Legends

Figure 1: The virtual city with the three experimental manipulations used for both encoding and retrieval.

Figure 2: An overview of the experimental design.

Figure 3: The retrieval of stored spatial layout was facilitated by the presence of a small interactive aerial view because it gave a real-time allocentric viewpoint-dependent representation including a visualized larger arrow.



Virtual city without an
interactive aerial view

Virtual city with a small scale
interactive aerial view

Virtual city with a large scale
interactive aerial view

Figure 2 .

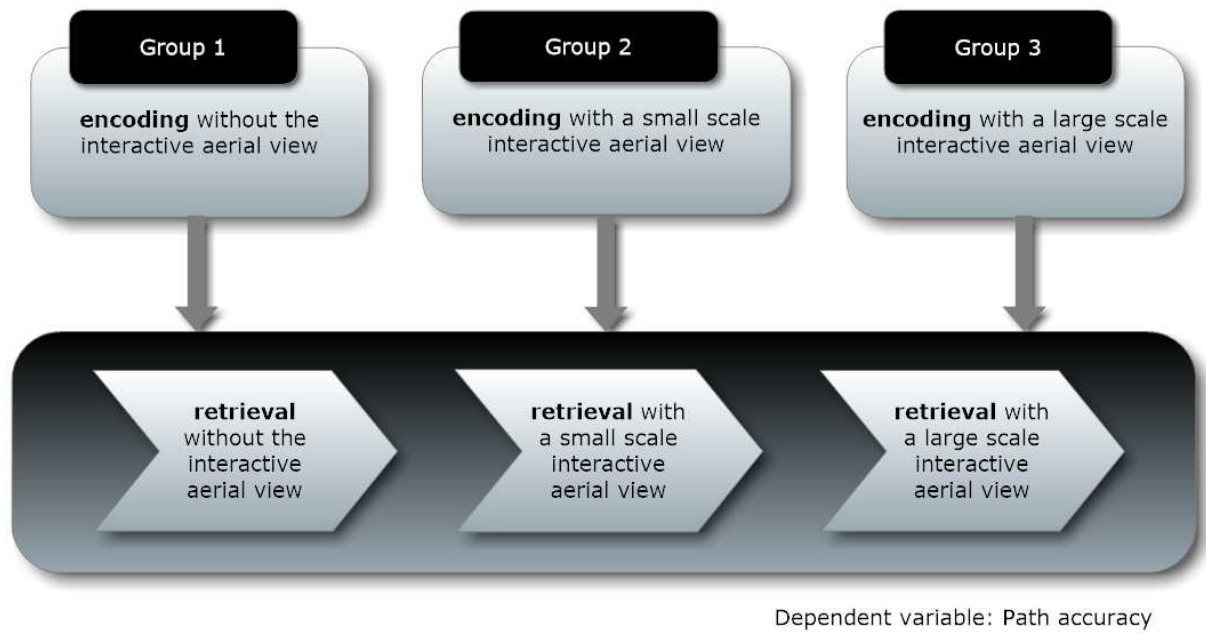


Figure 3 .

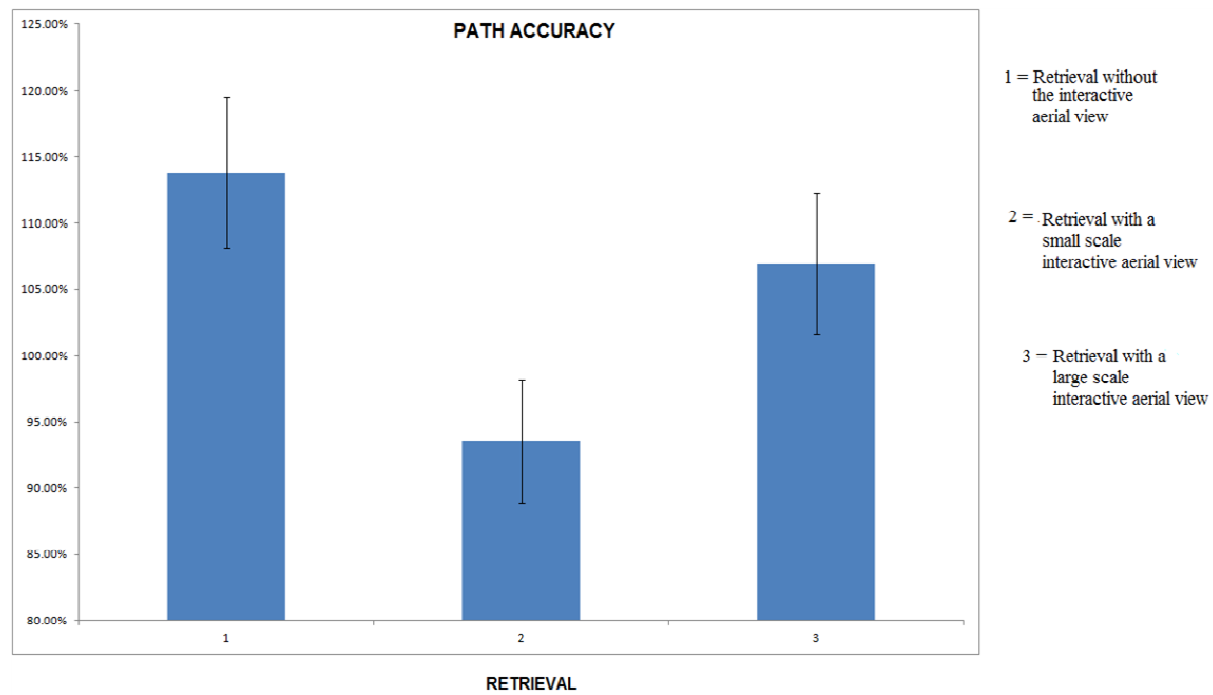


Figure 4 .