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Asymmetric learning transfer between imagined viewer- and object-rotations: Evidence of a hierarchical organization of spatial reference frames

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ABSTRACT

Neural resources subserving spatial processing in either egocentric or allocentric reference frames are, at least partly, dissociated. However, it is unclear whether these two types of representations are independent or whether they interact. We investigated this question using a learning transfer paradigm. The experiment and material were designed so that they could be used in a clinical setting. Here, we tested healthy subjects in an imagined viewer-rotation task and an imagined object-rotation task. The order of the tasks was counterbalanced across subjects. The results showed that subjects who did the viewer-rotation task first had fewer errors and shorter latencies of response in the object-rotation task, whereas subjects who did the object-rotation task first had little if any advantage in the viewer-rotation task. In other words, the results revealed an asymmetric learning transfer between tasks, which suggests that spatial representations are hierarchically organized. Specifically, the results indicate that the viewer-rotation task engaged allocentric representations and egocentric representations, whereas the object-rotation task engaged only egocentric representations.

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1. Introduction

1.1. Egocentric and allocentric reference frames

Performing voluntary actions, such as object manipulation and navigation, or imagining these actions entails representing and transforming spatial information. By necessity, spatial information is defined relative to a frame of reference. For example, the position of an object can be mapped in retino-centered coordinates, trunk-centered coordinates or relative to another object, among other possibilities. In other words, spatial information can be encoded in a variety of different frames of reference, which are categorized typically as either egocentric or allocentric (Zacks & Michelon, 2005). This labeling reflects the distinction between spatial coordinates that are defined relative to the self (e.g., retina, trunk) and those that are defined relative to an external reference (e.g., object, gravity, room). The role of these two types of reference frames depends on the context. For example, perspective-taking consists in imagining an object or scene from a different point of view than that of the viewer, whereas object mental rotation consists in imagining a change of orientation of an object from a fixed point of view. In other words perspective-taking consists in rotating the viewer reference frame relative to a stable allocentric frame of reference, whereas object mental rotation consists in rotating the object reference frame relative to a stable egocentric frame of reference. To avoid confusion, it is imperative to be clear about the reference frame that is transformed and the stable reference frame relative to which the transformation occurs. In the rest of this article we will use the terms egocentric and allocentric to indicate the stable frame of reference.

1.2. Brain resources for egocentric and allocentric information

It is well ascertained that processing spatial information in either egocentric or allocentric reference frames is associated with, at least partially, different brain networks (Zacks, 2008). For example, studies of brain-lesioned patients, and particularly patients with attentional neglect or spatial disorientation, have demonstrated that these two types of spatial representation can be impaired differentially (Chatterjee, 1994; Grimsen, Hildebrandt, & Fahle, 2008; Hillis et al., 2005; Holdstock, Mayes, Cezayirli, Aggleton, & Roberts, 1999; Kerkhoff, 2001; Marsh & Hillis, 2008; Medina et al., in press; Nyffeler et al., 2005; Pizzamiglio, Guariglia, & Cosentino, 1998). In addition, it was shown that memory of allocentric information was impaired in schizophrenia patients, whereas memory of egocentric information was not (Langdon, Coltheart, Ward, & Catts, 2001; Weniger & Irle, 2008).

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Similarly, neuroimaging studies have shown that egocentric and allocentric spatial representations were associated with different patterns of brain activation (Committeri et al., 2004; Galati et al., 2000; Gramann, Muller, Schonebeck, & Debus, 2006; Jordan, Schadow, Wuestenberg, Heinze, & Jancke, 2004; Keehner, Guerin, Miller, Turk, & Hegarty, 2006; Neggers, Van der Lubbe, Ramsey, & Postma, 2006; Wilson, Woldorff, & Mangun, 2005; Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Zacks, Vettel, & Michelon, 2003; Zaehle et al., 2007). However, the brain regions that were found to be related to one or the other type of spatial coding have been quite different across studies. Nevertheless, it can be inferred from these studies that there is a marked tendency for imagined object-rotation tasks to activate the dorso-parietal cortex and for perspective-taking tasks to activate to a greater degree the medio-temporal cortex (Zacks & Michelon, 2005). In addition, both types of tasks engage overlapping brain areas, in particular in the region of the occipito-parietal border as well as in the dorsal prefrontal cortex. Furthermore, several studies have found that processing mental images was associated with the activation of the premotor and primary motor areas during imagined object-rotation (Lamm, Windischberger, Moser, & Bauer, 2007; Richter et al., 2000; Tagaris et al., 1998; Wraga et al., 2005; Zacks, 2008) and imagined viewer-rotation (Creem et al., 2001; Wraga et al., 2005). The involvement of motor-related areas suggests that these tasks can be performed by imagining bodily actions on the object or displacements within the environment. In brief, the neuropsychological and neuroimaging studies have shown unequivocally that egocentric and allocentric representations are not subserved by a unitary neural process. However, these studies have led to diverging conclusions about whether the neural processes are completely dissociated (Zacks et al., 2003) or whether they are hierarchically organized (Zaehle et al., 2007).

1.3. Investigating the relation between egocentric and allocentric representations

The fact that brain lesions can affect egocentric or allocentric representations differentially is a necessary but not sufficient condition of independence. It leaves the possibility that the two types of representations interact at some stage of the process. In particular, it is important to consider that spatial information is encoded first by egocentric sensory systems (e.g., retina, muscle spindles) which can then be used to form allocentric representations (Andersen, 1997; Marr, 1980). In other words, allocentric representations are of higher-order than egocentric representations. Furthermore, an allocentric representation of space can be formed through integration of egocentric representations updated during spatial navigation (Etienne & Jeffery, 2004; Wang & Spelke, 2000). For these reasons, one could expect that tasks that require allocentric representations engage also egocentric representations, whereas the reverse would not be true. Here, we investigated this question by using a learning transfer paradigm. Even though the current study was done with healthy subjects, we designed the experiment and material so that it could be relatively easy to use in a clinical setting. The experiment is formed of an imagined object-rotation task and in an imagined viewer-rotation task. One group of subjects did the object-rotation task first, whereas the other group did the viewer-rotation task first. Then each group did the other task. If the two types of spatial representations were entirely independent, then which task is done first and which one is done second would be irrelevant. In contrast, if allocentric representations engaged egocentric representations but not *vice versa*, then the order of the tasks would matter. More specifically, the subjects who perform the viewer-rotation task first would engage allocentric and egocentric representations in the task, therefore the performance in the object-rotation task, which engage only egocentric representations, would bank on representations that were practiced in the viewer-rotation task. In contrast, the subjects who perform the object-rotation task first would engage only egocentric representations in the first task; therefore the viewer-rotation task would need the addition of non-practiced allocentric representations. In other words, even though both groups are expected to improve in the second task, the group performing the object-rotation task first would be at a disadvantage in the second task, relative to the group performing the viewer-rotation task first. For these reasons, we expect that when the viewer-rotation task is performed first, there would be a greater positive transfer to the object-rotation task, than when tasks are performed in the reverse order. The results show an asymmetric transfer between tasks that supports the hypothesis that allocentric representations engage egocentric representations, but not the reverse.

2. Methods

2.1. Participants

Twenty-eight subjects participated in this study (mean age = 25.6 years, age range = 18–34 years; 13 males, 15 females). Six males and eight females did the tasks in the order viewer- then object-rotation, whereas seven males and seven females did the tasks in the reverse order. All participants gave their informed consent to participate in the study. The experimental protocol was approved by the Institutional Review Board of the Geneva University Hospitals.

2.2. Material

Instruction stimuli were printed on paper sheets. They represented a perspective view of a round table with four differently colored discs on its surface, placed at equal intervals and at equal distance from its center. An arrow, peripheral to the table, pointed towards its center from an angle of 0°, ±60°, ±120° or 180° relative to the direction ahead of the subject. Negative angles were in the counterclockwise direction, whereas positive angles were in the clockwise direction. In brief, there were six instruction stimuli printed on separate sheets (all instruction stimuli are provided in Supplementary material). Fig. 1A shows one instruction stimulus, whereas Fig. 1B shows the six directions tested.

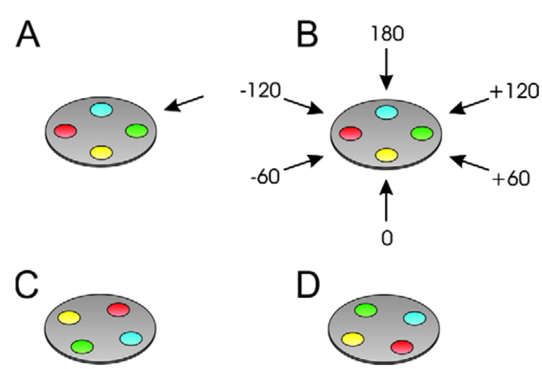

Fig. 1. (A) Instruction stimulus with the arrow at +120°. In the *viewer-rotation task*, the subjects were instructed to imagine that they turned around the table up to the point indicated by the arrow. In the *object-rotation task*, the subjects were instructed to imagine that they rotated the table until the point indicated by the arrow was in front of them. In both cases, they had to select on a response sheet the view of the table after the imagined rotation. (B) Instruction stimulus with the six angles tested. (C) One of the rotated views to select. It corresponds to the correct response for the instruction stimulus in A. (D) One of the views of the mirror-imaged table. All instruction stimuli and response sheets are provided as Supplementary material.

Ten response sheets were prepared with 12 perspective representations of the round table on each one. Six representations corresponded to views of the same table as the instruction but from different points of view, whereas six representations were different points of view of a mirror-image table. The 12 perspectives representations were arranged pseudo-randomly on the sheet in four rows and three columns (all response sheets are provided in Supplementary material). Fig. 1C shows one of the rotated views, whereas Fig. 1D shows one of the views of the mirror-image table. Each perspective view was labeled with a letter (i.e., A–L) to identify it. The response sheets were prepared so that the view to be selected had the same probability to be in any row and column on the sheet. A chronometer was used to record the response time (RT).

2.3. Conditions

The experiment consisted of the viewer-rotation task and the object-rotation task, which differed only by the instruction given to the subject. The two tasks were performed in counterbalanced order across subjects and in separate sessions of approximately 1 h each. The interval between sessions was flexible to emulate the variability encountered in clinical settings. It was not significantly different between the two groups of subjects differentiated by task-order (Kolmogorov–Smirnov $Z = 0.756$, $p = 0.617$). The median interval between sessions was 5 days (Tukey hinges = 1 and 9 days).

In the viewer-rotation task, subjects were instructed to imagine themselves turning around the table until they had reached the location indicated by the arrow. In contrast, in the object-rotation task, subjects were instructed to imagine that they rotated the table until the location indicated by the arrow was in front of them. In either case, the subjects had to select on the response sheet the view that represented the table after the imagined rotation. They indicated their choice by saying the letter printed next to the selected view.

The trials were organized in a randomized block order. Each task was formed of ten blocks of the six instruction stimuli. Two sequences of trials were retained to prepare two binders with sixty information stimuli and two binders with sixty response sheets (the sequence of trials for each task-order can be found in the Supplementary material). For each trial, the instruction stimulus was presented by flipping a page of the binder. After the subject had examined the instruction stimulus, a page of the response sheets binder was flipped as well. The subjects were told that they had the time they needed to respond. Nevertheless, the latency of response was measured between the flip of the response sheet and the subject response to examine whether it was affected by the experimental conditions.

2.4. Data analyses

The proportion of errors, P, computed over N trials was transformed (P^*) for averaging and analyses using Anscombe angular transform to normalize the distribution and control the variance (Chanter, 1975):

$$P^* = \sin^{-1}\left(\sqrt{(N \cdot P + 3/8)/(N + 3/4)}\right) \quad (1)$$

The average response time, $\overline{\mathrm{RT}}$, of N_C correct responses was computed using the harmonic mean which is robust to potential outliers (Ratcliff, 1993):

$$\overline{\mathrm{RT}} = N_C \bigg/ \sum_{i=1}^{N_C} 1/\mathrm{RT}_i \quad (2)$$

The proportion of errors and the average response time were both analyzed using a Linear Mixed Model (LMM; West, Welch, & Gałecki, 2007) with the fixed factors gender, task-order, task and instruction-angle. The last two factors were repeated-measures within the factor subject. The repeated-measures covariance matrix of the model was selected using Schwarz's Bayesian criterion (Littell, Pendergast, & Natarajan, 2000). In addition, we tested the hypothesis that the effect of task-order was greater in the object-rotation task than in the viewer-rotation task. This specific comparison was made using a one-tailed t-test on the basis of the LMM estimates. Finally, the relation between the performance in the first task and the performance in the second task was analyzed on the results of each subjects averaged across instruction-angle. This analysis was performed on the proportion of errors and RT separately using a LMM with task-order as factor, the corresponding performance in the first task as covariate, and the interaction task-order × covariate. Effects at $p < 0.05$ level were considered significant. All the analyses were performed using SPSS 15.0 (SPSS Inc., Chicago IL).

3. Results

3.1. Errors

On average subjects made 6.1% errors (range = 0–35%; chance level for errors = 91.7%). The LMM analysis was performed using the compound symmetry model for the within-subject covariance matrix (see Methods). Fig. 2 illustrates the statistically significant effects. The analysis indicated that the proportion of errors varied across instruction-angle ($F(5, 264.0) = 2.565$, $p = 0.027$). Fig. 2 (left) shows that the proportion of error had a seagull profile across instruction-angle, that is, it was generally smaller for the 0° and 180° than for the intermediate angles of ±60° and ±120°. However, this modulation across angle was affected by task-order (task-order × instruction-angle: $F(5, 264.0) = 2.713$, $p = 0.021$). As can be seen in Fig. 2 (left), the proportion of errors was greater at the intermediate angles of ±60° for the subjects who did the object-rotation task first (O–V), than for those who did the viewer-rotation task first (V–O). The strongest statistical effect, though, was due to the differential effect of task-order on task performance (task-order × task: $F(1, 264.0) = 21.688$, $p < 0.001$), which is illustrated in Fig. 2 (right). We analyzed the interaction task-order × task further. First, the proportion of errors for the object-rotation task performed first was slightly higher than the proportion of errors for the viewer-rotation task performed first. However, this difference was not significant ($F(1, 26.0) = 0.777$, $p = 0.386$), which suggests that the two tasks were not *a priori* different in terms of difficulty. In addition, we performed a custom hypothesis test that showed that the effect of task-order was sig-

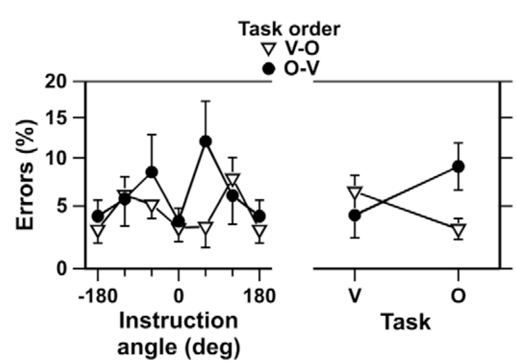

Fig. 2. Average proportion of errors for the statistically significant effects. (Left) Task-order × instruction-angle. (Right) Task-order × task. Error bars represent the standard error of the mean; in some cases they are plotted only on one side to limit clutter. The ordinate is an angular scale (see Methods). The −180° and +180° data points are the same, but were duplicated for symmetry.

nificantly greater for the object-rotation task than for the viewer-rotation task (one-tailed t-test(62.10) = 3.248, $p < 0.001$). There was no other statistically significant effect of the LMM analysis (all the results of the LMM analysis are provided in the Supplemental material Table S1; note that the LMM analysis performed on the untransformed proportion of errors provided the same significant effects). In summary, these results showed that there was an asymmetric transfer from one task to the other, with an advantage in term of proportion of errors for the subjects who did the viewer-rotation task first relative to those who did the object-rotation task first.

We performed additional analyses to identify the type of errors that the subjects made. For this purpose we divided the errors into two categories: (1) congruent errors that resulted from the selection of a view from an incorrect angle and (2) incongruent errors that resulted from the selection of one of the mirror-image views. We found that most of the errors were congruent errors (70.4% of all errors; chance level of congruent errors among all errors = 45.5%) rather than incongruent errors ($\chi^2(1) = 41.93$, $p < 0.001$). In other words, most errors were due to the selection of a view from an incorrect direction rather from the selection of an 'impossible' view.

Furthermore, we analyzed whether congruent errors occurred by selecting a view close to the correct one or whether any incorrect view had been selected. For this purpose, we categorized congruent errors in adjacent errors and non-adjacent errors. An adjacent error corresponded to the selection of a view that was close from the correct one (i.e., ±60° from the correct view), whereas a non-adjacent error corresponded to the selection of any other congruent view. We found that congruent errors were composed mostly of adjacent errors (92.1% of congruent errors; chance level of adjacent errors among congruent errors = 40.0%) rather than of non-adjacent errors ($\chi^2(1) = 126.4$, $p < 0.001$). Consequently, congruent errors were composed mostly of relatively small angular errors.

We analyzed also the incongruent errors further, by considering that they could be partially correct if two diametrically opposed color discs were in the expected locations whereas the other two were not. We found that incongruent errors were composed mostly of partially correct views (86.9% of incongruent errors; chance level of partially correct views among incongruent errors = 33.3%) and less often of completely incorrect ones ($\chi^2(1) = 53.8$, $p < 0.001$). Consequently, even when subjects selected a view that could not be obtained through a planar rotation of the instruction stimulus, generally part of it was correctly oriented. In summary, all these error cases indicate that most errors were relatively similar to the correct response. This result implies that in most cases even when the response was erroneous subjects had attempted to perform the task. The errors were often the results of inaccurate rotations and in some cases of transformations of only part of the object; infrequently they were a complete failure of the transformation process.

3.2. Response time

The LMM analysis was performed using the heterogeneous compound symmetry model as within-subject covariance matrix. Fig. 3 shows the effects that were statistically significant. The analysis indicated that RT was significantly different across instruction-angle ($F(5, 74.7) = 9.168$, $p < 0.001$). Fig. 3 (left) shows that RT had a seagull shape across instruction-angle, globally similar to that of the proportion of errors: it was shorter for the 0° condition than for any other condition, and it was longer for the intermediate angles of ±60° and ±120° than for 180°. However, the effect of instruction-angle was dependent on the task (task × instruction-angle: $F(5, 98.8) = 3.025$, $p = 0.014$). It can be noticed in Fig. 3 that, while for the viewer-rotation task, RT increased sharply from 0° to ±60° and decreased slightly afterwards, for the object-rotation task, it increased more progressively from 0° to ±120° and then decreased strongly at 180°. This differential effect of task on the relation between RT and instruction-angle suggests that different time-consuming processes of mental rotation were engaged in the two tasks. As for the proportion of errors, the strongest statistical effect was the due to the interaction task × task-order ($F(1, 72.6) = 53.673$, $p < 0.001$). There was no other statistically significant effect (all the results of the LMM analysis are provided in the Supplemental material Table S2). The custom hypothesis test indicated that the effect of task-order was significantly greater in the object-rotation task than in the viewer-rotation task (one-tailed t-test(48.74) = 2.540, $p = 0.007$). To sum up, the RT results were consistent with the errors results; both measures showed that there was an advantage for the subjects who did the viewer-rotation task first relative to those who did the object-rotation task first.

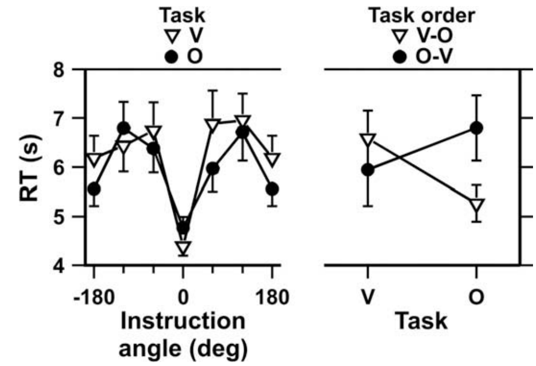

Fig. 3. Average response time for the statistically significant effects. (Left) Task × instruction-angle. (Right) Task-order × task. The conventions are the same as for Fig. 2.

3.3. Relation between performance in the first and the second task

We examined whether the performance (i.e., percentage of errors and RT) in the second task was related to the performance in the first task, and whether this relation differed depending on task-order. For this analysis, the data of each subject were averaged across instruction-angle. These data are plotted in Fig. 4. It can be noticed that, as expected, the data points are predominantly below the diagonal, which indicates that the performance in the second task was generally more accurate and the responses faster than in the first task. To examine the relation in more details, we analyzed the model with the factor task-order, the performance in the first task (i.e., percentage of errors or RT) as covariate, and the interaction between task-order and covariate. The model fitted the data significantly for both performance measures, even though the fit was noticeably better for RT than for the percentage of errors (percentage of errors: $R^2 = 0.527$, $F(3, 24) = 8.896$, $p < 0.001$; RT: $R^2 = 0.858$, $F(3, 24) = 48.381$, $p < 0.001$). The fitted model regarding the (Anscombe-transformed) percentage of errors was $Y = 0.175 + 0.247X$ for the V–O group and $Y = 0.009 + 0.754X$ for the O–V group; whereas the fitted model on RT was $Y = 1.432 + 0.580X$ for the V–O group and $Y = -0.800 + 0.978X$ for the O–V group.

As expected, there was a positive slope that related the percentage of errors in the second task to the percentage in the first task ($F(1, 24) = 14.006$, $p = 0.001$); and similarly for RT ($F(1, 24) = 119.356$, $p < 0.001$). However, the slopes were steeper for the subjects in the O–V group than for those in the V–O group. This differentiation of the slopes between groups was close to, but did not reach, statistical significance for the proportion of errors

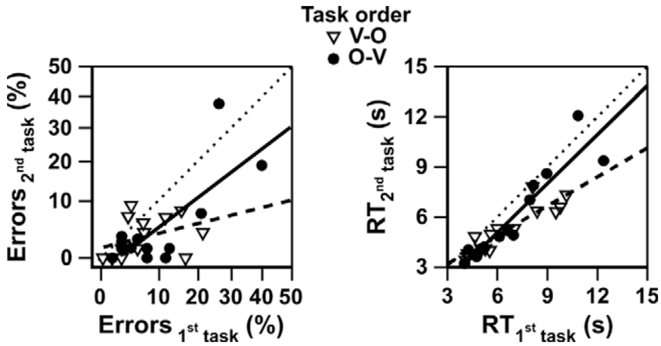

Fig. 4. (Left) Relation between percentage of errors in the second task and percentage of errors in the first task for each subject in the two task-order groups. (Right) Relation between RT in the second task and RT in the first task for each subject in the two task-order groups. The dotted line shows the diagonal as a reference. The regression line is plotted as a dashed line for the V–O group and as a continuous line for the O–V group.

($F(1, 24) = 3.584$, $p = 0.070$), whereas it was statistically significant for RT ($F(1, 24) = 7.796$, $p = 0.010$). This analysis shows that the performance of subjects in the O–V group did not gain as much in the second task as that of subjects in the V–O group.

4. Discussion

We investigated whether there was evidence of independence or of interaction between egocentric and allocentric representations. To this end we tested subjects in an imagined object-rotation task and in an imagined viewer-rotation task. The order of the tasks was counterbalanced across subjects. The competing hypotheses were that, if the two types of spatial representations were entirely independent, then the order of the tasks would not matter; in contrast, if allocentric representations require egocentric representations, but not *vice versa*, then the order of the tasks would make a difference. Specifically, we would expect that when the viewer-rotation task was performed first, there would be a greater transfer to the object-rotation task, than when the tasks were performed in the reverse order. The results were consistent with the latter hypothesis. They showed that subjects who did first the viewer-rotation task had fewer errors and shorter latencies of response in the object-rotation task, whereas subjects who did first the object-rotation task had little if any advantage on the viewer-rotation task. In addition, the analysis of the relation between the performance in the second task relative to the performance in the first task showed that the subjects who did the viewer-rotation task first tended to improve more in the second task than the subjects of the other group. In brief, the results of the different analyses converged in revealing an asymmetric transfer effect between tasks, which implies that spatial representations are hierarchically organized. Specifically, the results suggest that while the object-rotation task relied on egocentric representations, the viewer-rotation task required both egocentric and allocentric representations.

This conclusion is consistent with functional magnetic resonance imaging studies of spatial coding (Committeri et al., 2004; Galati et al., 2000; Zaehle et al., 2007). These studies showed that while egocentric coding required the posterior parietal and frontal premotor regions, allocentric coding recruited in addition the ventral occipito-temporal region. In other words, these results indicate that the neural network engaged for egocentric coding is a subset of the network for allocentric coding. However, as mentioned in the introduction, the patterns of brain activity that have been determined to be associated with egocentric and allocentric coding have been variable across studies and they do not always show this hierarchical organization (Wraga et al., 2005; Zacks et al., 2003). Nonetheless, there is evidence in support of such an organization from other sources as well. For example, perspective-taking ability, which requires allocentric coding, becomes effective at a later stage during child development than egocentric coding (Huttenlocher & Presson, 1973; Piaget & Inhelder, 1967). By the same token, adult performance declines more rapidly with age in allocentric viewer-rotation tasks than in egocentric object-rotation tasks (Inagaki et al., 2002). Finally, many animals (including humans) can form a representation of a small environment relying only on egocentric information obtained during self-displacement (Etienne & Jeffery, 2004; Wang & Spelke, 2000).These studies indicate that allocentric representations can be formed through the integration of egocentric representations. Consequently, this ensemble of studies support the idea that allocentric representations are built upon, and therefore are of higher-order than, egocentric representations.

Even though the problem of imagining a point of view by rotating mentally an object is equivalent to turning around it mentally, the behavioral results indicate that these two operations were not performed in the same manner. First, we found that error rates were greater and response times were longer for the object-rotation tasks than for the viewer-rotation task when these tasks were performed first. These results are consistent with those of many other studies (Wraga, Creem, & Proffitt, 1999). However, we found also that it was not always the case. Indeed, subjects who did the viewer-rotation task first, had the best performance of all in the object-rotation task. A similar effect of task-order was noticed in another study (Amorim & Stucchi, 1997). However, the order of the tasks was a consequence of the experimental design and not of primary interest to their study, for this reason Amorim and Stucchi (1997) did not elaborate on the possible meaning of this effect regarding the relation between egocentric and allocentric representations. In summary, the level of performance is not related simply to the task but is dependent on task-order as well. We suggest that the subjects who did the viewer-rotation task first had engaged both the allocentric and egocentric representations systems. This double representation of spatial information gave them an advantage during the object-rotation task, since it requires an egocentric representation which had already been trained with the same material. In contrast, the subjects who did first the object-rotation had engaged only the egocentric representation and were 'naïve' relative to the allocentric representation when they did the viewer-rotation task. For this reason, these latter subjects did not have a very different performance in the viewer-rotation task than those who did it as the first task.

On a different topic, even though the proportion of errors was the main dependent variable of this study, we measured RT to obtain potentially additional information. RT was not considered as important as the proportion of errors because its measurement had two main limitations. First, it was limited in accuracy by the manual procedure, but its main limitation was that it included, not only the process of mental transformation of interest, but also the search of the view on the response sheet, which was possibly quite complex. For all these reasons, we were expecting that the effects with RT would be blurred and possibly non-significant. However, it turned out that they were quite clear and consistent with those of the proportion of error. The results of the statistical analyses indicated that the effects on RT were quite reliable and consistent across subjects. Furthermore, the limitations on the measurement of RT were the same in all conditions and, therefore, they cannot explain the significant differences in RT between conditions. In addition, we found that the relation between response time and angle of transformation was different between the two tasks. In the object-rotation task, RT increased monotonically with instruction-angles from 0 to 120° and then decreased at 180°. Similar non-monotonic relations between RT and angle in object-rotation tasks have been reported in other studies (Zacks et al., 2003).

This pattern is consistent with the hypothesis that the object-rotation task was performed by mentally rotating the image of the display for angles smaller than 180° (Shepard & Cooper, 1982), whereas a non-rigid transformation was performed for the 180° angle. In contrast, in the viewer-rotation task RT was much shorter for 0° than for all the other angles without much change otherwise. Several studies have shown that RT was less dependent on the angle of rotation in perspective-taking tasks than in object mental rotation tasks (Amorim & Stucchi, 1997; Hayward, Zhou, Gauthier, & Harris, 2006; Keehner et al., 2006; Wraga, Creem, & Proffitt, 2000; Zacks et al., 2003). The step-like transition of RT between 0° and all the other angles suggests that in this task the spatial transformation was not analogous to a rotation, but instead was akin to a discrete operation. In such a case, what changes the latency is whether or not there is a transformation to perform rather what is the angle of the transformation. In summary, the results indicate that imagined object-rotation and imagined viewer-rotation were performed by time-consuming processes with different properties. Given that egocentric and allocentric representations engage different neural networks, it may not be surprising that they have different functional properties.

One of the limitations of the current study is that the tasks were relatively easy for healthy subjects. For this reason, the error rates were fairly low and possibly a ‘floor’ effect might have occurred. However, in all conditions the proportion of error was not uniform across instruction-angle and had higher values for the intermediate angles (i.e., 60 and 120°), which indicates that the performance was not entirely floored. However, the question is whether the ‘floor’ effect could have contributed to the asymmetric effect observed. We can see that this cannot be the case. Indeed, the lowest overall error rate was obtained in the object-rotation task by the subjects who did the viewer-rotation task first (Fig. 2). If the error rates could have gone lower, it would have increased the asymmetry of the transfer between tasks. In other words, the ‘floor’ effect worked against the asymmetry described and therefore it cannot be at the source of it.

Another issue to consider is whether the subjects actually performed the second task using the new instruction rather than performing it using the instruction given in the first session. Subjects could be inclined to do that if, for example, one task was particularly more difficult than the other. In this case, the subjects who did the easier task first might want to perform the task during the second session following the first set of instructions rather than the more difficult instructions. Such a scenario could lead to an asymmetry in the results such as the one observed. However, there are two lines of evidence that are not consistent with this interpretation. First, there was no significant difference in the proportion of errors for the tasks performed first. This suggests that the two tasks were not very different in terms of difficulty, which means that there was no obvious reason to prefer one set of instructions over the other one. Second, the profile of RT across instruction-angle varied with task, which suggests that the subjects performed a mental process of transformation that was task-dependent. In other words, subjects changed their way to do the task depending on the instructions.

The use of imagined object- and viewer-rotation tasks to investigate the abilities of brain-lesioned patients and healthy subjects has provided important information regarding the brain processes subserving spatial information. Recently, some studies have indicated that these tasks are potentially useful for investigating the pathophysiology of psychosis and in particular schizophrenia. The dissociation between egocentric memory and allocentric memory in schizophrenia patients (Weniger & Irle, 2008) is consistent with the abnormal distribution of neural activity in the lateral occipital region, which is associated with allocentric object recognition (Wynn et al., 2008). In addition, it has been suggested that the impairment of schizophrenia patients with inferring other persons' mental states (i.e., Theory of Mind deficit) is linked to an impairment with allocentric representations (Langdon et al., 2001). These studies raise the possibility that the investigation of spatial reference frames will provide useful information regarding the difficulties in perspective-taking of schizophrenia patients.

In conclusion, the results show an asymmetric transfer between imagined viewer- and object-rotation tasks. This pattern supports the hypothesis that the viewer-rotation task engaged allocentric representations and egocentric representations, whereas the object-rotation task engaged only egocentric representations.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bandc.2009.08.001.

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