# Modulation of Spatial Orientation Processing by Mental Imagery Instructions: A MEG Study of Representational Momentum

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## Abstract

■ Under appropriate conditions, an observer's memory for the final position of an abruptly halted moving object is distorted in the direction of the represented motion. This phenomenon is called "representational momentum" (RM). We examined the effect of mental imagery instructions on the modulation of spatial orientation processing by testing for RM under conditions of picture versus body rotation perception and imagination. Behavioral data were gathered via classical reaction time and error measurements, whereas brain activity was recorded with the help of magnetoencephalography (MEG). Due to the so-called inverse problem and to signal complexity, results were described at the signal level rather than with the source location modeling. Brain magnetic field strength and spatial distribution, as well as latency of P200m evoked fields were used as neurocognitive markers. A task was devised where a subject examined a rotating sea horizon as seen from a virtual boat in order to extrapolate either the picture motion or the body motion relative to the picture while the latter disappeared temporarily until a test-view was displayed as a final orientation candidate. Results suggest that perceptual interpretation and extrapolation of visual motion in the roll plane capitalize on the fronto-parietal cortical networks involving working memory processes. Extrapolation of the rotational dynamics of sea horizon revealed a RM effect simulating the role of gravity in rotational equilibrium. Modulation of the P200m component reflected spatial orientation processing and a non-voluntary detection of an incongruity between displayed and expected final orientations given the implied motion. Neuromagnetic properties of anticipatory (Contingent Magnetic Variation) and evoked (P200m) brain magnetic fields suggest, respectively, differential allocation of attentional resources by mental imagery instructions (picture vs. body tilt), and a communality of neural structures (in the right centro-parietal region) for the control of both RM and mental rotation processes. Finally, the RM of the body motion is less prone to forward shifts than that of picture motion evidencing an internalization of the implied mass of the virtual body of the observer. ■

## INTRODUCTION

Is visual motion perception and imagination influenced by the frame of reference (cognitive set) used to process the spatial orientation input? Is the cognitive dynamics of environment- versus self-motion extrapolation the same? In order to address these two issues we built a paradigm that elicits representational momentum (RM) and tested the constraints introduced by cognitive set on RM using the same visual stimuli but two different mental imagery instructions in order to drive the perceptual interpretation of the spatial orientation input. In addition, we looked for neural correlates of RM using measurement of brain magnetic activity by magnetoencephalography (MEG).

Therefore, the aim of this study is two-fold. On the one hand, we are testing the hypothesis that cognitive set modulates representational momentum. Representational momentum is the tendency for memory to be distorted in the direction of an implied transformation (Hubbard, 1995; Freyd, 1987). For instance, the remembered position of a horizontally moving target is usually displaced in front of and below the actual position of that target (Hubbard, 1990). This is suggestive of an internalization of environmentally invariant physical principles into the cognitive system (Hubbard, 1998;

Shepard, 1984), i.e., momentum and gravitational attraction. Although several other variables are known to affect RM, such as implied velocity, implied friction, and centripetal force (Hubbard, 1995), no data exist regarding an effect of cognitive set. Instead of examining RM on the basis of memory tests, we used a mental extrapolation paradigm (Li & Franklin, submitted; Finke & Freyd, 1989; Finke & Shyi, 1988). Our hypothesis was that the inertial properties of RM would be affected by the current cognitive set used to interpret the spatial orientation visual input, i.e., extrapolating picture versus body motion.

On the other hand, we are looking for a neural correlate of RM. Although the literature on the neural basis of mental imagery processes such as image generation and scanning (for a review, see Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998) or mental rotation (e.g., Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Alivisatos & Petrides, 1997; Cohen et al., 1996) is quite rich, it is not the case for RM. Following a principle of neurofunctional thrift, it can reasonably be hypothesized that RM builds on neurocognitive networks engaged in motion perception or mental rotation. Along those lines, the existing neuroimaging studies of RM, using fMRI, showed an activation in human MT/MST (Kourtzi & Kanwisher, 2000) together with precuneus (Senior et al., 1999) when viewing static photographs with implied motion (e.g., a man jumping). The MT(V5) and MST areas are typically devoted to visual motion processing (Barton et al., 1996) and also involved in mental rotation tasks (Cohen et al., 1996). The present study required a method that offers the possibility to measure brain activity within consecutive periods of 200 msec. Furthermore, we needed a method that allows selective analysis of trials based on behavioral performance. These are the reasons why we used MEG. And in fact, it turned out that the effect of cognitive set was only present at a certain step of information processing and some effects were only present in particular trial classes. Whole-head MEG

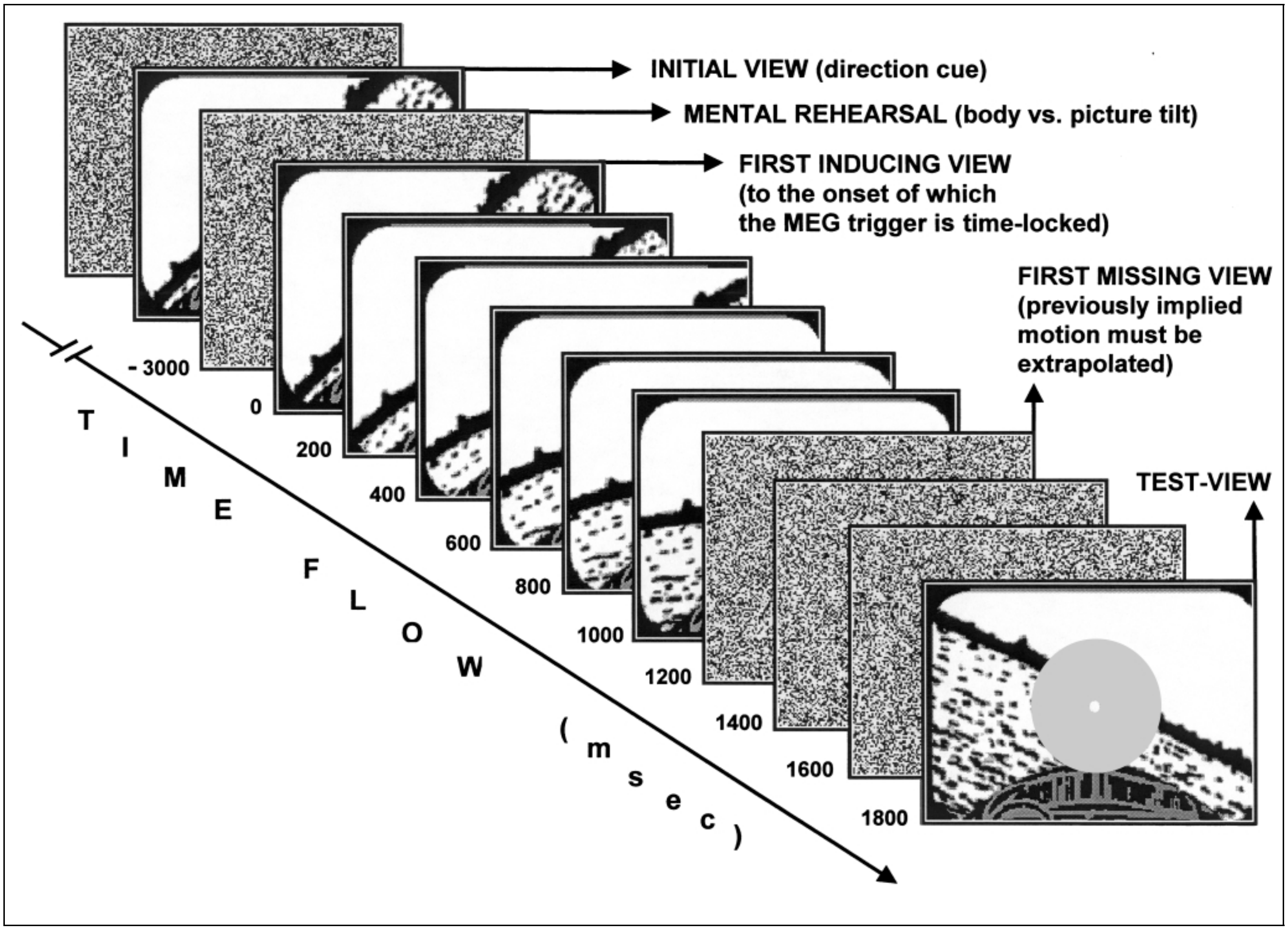

**Figure 1.** An example of stimuli sequence. The initial view, acting as a direction cue, lasted until the subject pressed a pedal to indicate that he/she had mentally set into either a "picture tilt" or his/her corresponding "body tilt." Then, the random pixels image of this view was displayed for 3 sec. The number of the subsequent inducing views varied between 6 and 8. Finally, a test-view was displayed for 200 msec and followed by its random pixels counterpart for 2.8 sec. The task was to indicate if the orientation referred by the test-view was the one that would be expected according to the momentum of the inducing views extrapolated mentally during the missing views.

(Lounasmaa, Hämäläinen, Hari, & Salmelin, 1996) provides very good temporal resolution (1 msec) and a fair spatial resolution (≈ 5 mm), especially when localizing single dipolar current source, and thereby may even help to improve fMRI brain mapping results (Beisteiner et al., 1997). However, when the MEG signal becomes complex, due to the so-called inverse problem (Näätänen, Ilmoniemi, & Alho, 1994), it is wiser to describe the results at the signal level rather than look at the infinite number of source solutions (for a discussion, see Okada & Salenius, 1998). Therefore, although we did not determine the source locations, we hypothesized that changes in the strength and spatial distribution of evoked fields would reflect the modulation of spatial orientation processing by mental imagery (cognitive set and RM).

In the last decades, the study of subjective visual vertical (Mittelstaedt, 1988) provided a unique paradigm in understanding the static and dynamic aspects of spatial orientation processing. For this reason, we found it interesting to investigate the effect of mental imagery on brain processing of spatial orientation around the roll axis, by having the subjects interpret visual motion input as either due to the rotation of the picture, or to a roll tilt of their body. Instead of using two different types of stimuli, like in studies comparing mental rotation of object versus body parts (Kosslyn et al., 1998), in order to avoid a confounding between a reference frame and stimuli-type effects, we used a similar visual input but different reference frame interpretations via mental imagery instructions (Amorim & Stucchi, 1997). Therefore, our subjects observed the display of a tilted sea horizon, as seen from a virtual boat, in order to set mentally into either a visual (''picture'' tilt) or a motor (''body'' tilt) imagery (Jeannerod, 1994). Then, the horizon rotated and the subjects would extrapolate either the picture or their corresponding body motion while entering a ''virtual fog'' until a last view of the tilted horizon was displayed (test-view), which the subjects either decided to accept or not as the expected final orientation (cf. Figure 1).

In order to examine the neural correlates of RM and reference frame manipulation, our rationale was first to find a marker for spatial orientation processing, and then observe how it might be modulated by mental imagery (cognitive set and RM). On the one hand, mental imagery can be considered as an attentional state (Farah, 1989), especially in our task where imagery instructions are driving the subjects attention toward a given reference frame. On the other hand, event-related potential studies (Rugg & Coles, 1996) showed that P200 component is modulated by visual-spatial attention (Mangun & Hillyard, 1996) and mental imagery processes (Farah, Péronnet, Gonon, & Giard, 1988). Therefore, the neuromagnetic P200 component (P200m) seemed a good candidate as neurocognitive marker in order to observe a modulation of

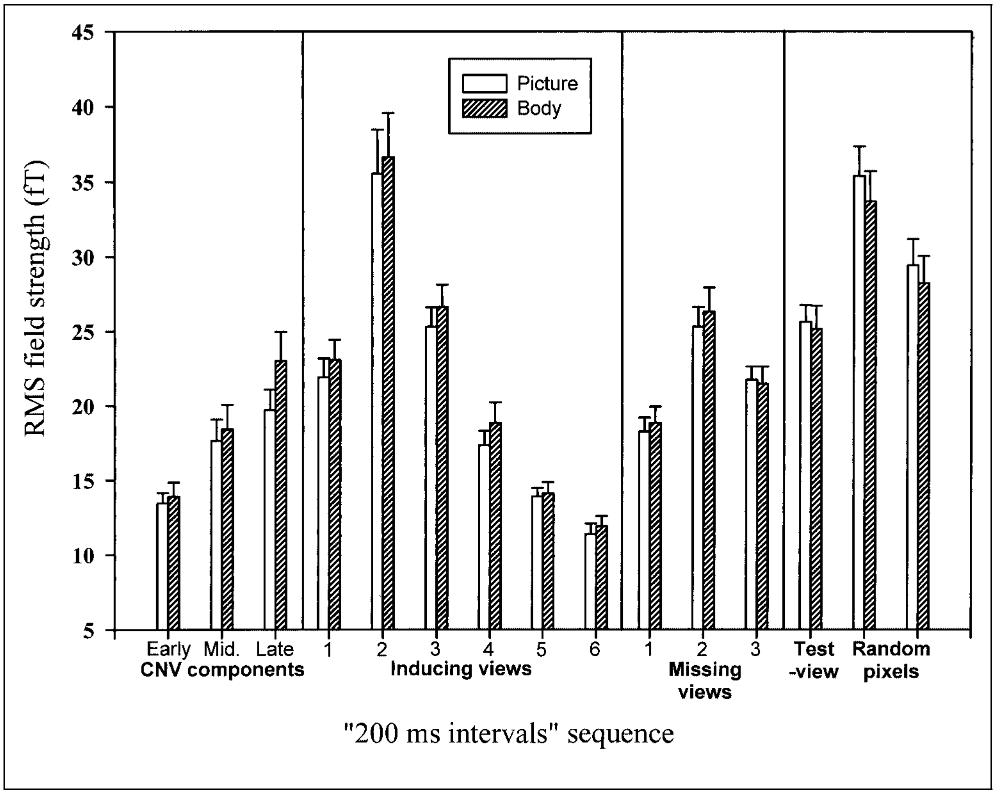

**Figure 2.** Mean results (± *SEM*) for root mean squared magnetic field strength (fT) as a function of the sequence of events displayed to the subjects (see Figure 1), for both mental imagery conditions.

spatial orientation processing. In particular, a neural correlate of RM effect would be evidenced by comparing, on the basis of the behavior, the evoked response for trials showing RM effect with those showing no such an effect.

## RESULTS

The modulation of spatial orientation processing by mental imagery instructions was observed in both the behavioral and brain activity levels. Therefore, for clarity of exposure, behavioral and MEG results (broken into 200-msec time intervals) will be presented together and following the sequence of events displayed to the subjects (cf. Figures 1 and 2).

### Mental Rehearsal of a Spatial Orientation Cognitive Set (Picture vs. Body Tilt)

As described in Methods, before the sea horizon rotated (inducing views), the subjects interpreted an initial view (direction cue) tilted 45° (cf. Figure 1) either as due to his/her body being virtually tilted (“body tilt” condition) or the picture of the horizon being tilted (“picture tilt”).

From a behavioral perspective, it took significantly [$F(1,12)6.43$, $p = .026$] longer for the subjects to set mentally into a body-tilt ($M = 2.92$; $SD = 1.82$ sec) than a picture-tilt mode ($M = 2.42$; $SD = 1.66$ sec). This latency was not affected by the tilt direction [$F(1,12) < 1$; *ns*]. However, we expected that this latency for mentally setting into an initial orientation, either clockwise (CW) or counterclockwise (CCW), might be affected by the final orientation of the previous trial. Accordingly, if the test-view orientation of the preceding trial was CW, for example, it would take more time to mentally set into an initial CCW orientation than one CW. Therefore, we compared the mental set latencies of trials for which the starting orientation was “compatible” with that of the test-view of the preceding trial, against those which were “incompatible.” The results displayed in Table 1 showed a significant [$F(1,12) = 9.45$, $p = .01$] effect of compatibility for the “picture imagery” condition but not for the “body imagery” condition [$F(1,12) < 1$; *ns*].

**Table 1**. Mean Latency (*SD* Between Parentheses) for Setting Mentally into a Starting Orientation Depending on Its Compatibility with the Orientation of the Preceding Test-View, for Each Mental Imagery Condition

| *Mental Imagery* | *Compatible Orientation* | *Incompatible Orientation* |
|---|---|---|
| Picture | 2.33 (1.58) | 2.49 (1.71) |
| Body | 2.85 (1.76) | 2.93 (1.82) |
| Mean | 2.59 (1.70) | 2.71 (1.78) |

The display of the direction cue was terminated by the subject and followed by a random pixels view for 3 sec just before the sequence of views inducing the rotation of the sea horizon. As described in Methods, for each trial the entire MEG recordings were triggered by the onset of the first inducing view. The 600-msec pre-trigger interval (falling during the random pixels display) was divided for analysis. Results showed a significant increase of field strength during the three 200-msec pre-trigger intervals [$F(1.61,19.33) = 32.88$; $p < .0001$], suggesting the presence of a Contingent Magnetic Variation (CMV) (Deecke, 1996; Elbert, Rockstroh, Hampson, Pantev, & Hoke, 1994). As illustrated in Figure 2, the brain field strength increased more rapidly for the body rather than the picture imagery as a function of the CMV components [$F(1.94,23.27) = 3.90$; $p = .036$]. More precisely, this effect of imagery condition on field strength showed up during the last 200-msec pre-trigger interval [$F(1,12) = 6.58$; $p = .025$], which is the late CMV component (Hultin et al., 1996). The spatial distribution of field strength was significant during this late component [$F(3.5,41.99) = 3.42$; $p = .021$]. The effect of imagery condition was observed for the right precentral [$F(1,12) = 5.13$; $p = .043$] and right inferior-parietal [$F(1,12) = 6.91$; $p = .022$] regions.

### Brain Response to Induced Motion

The number of inducing views varied from six to eight (see Methods section). Due to the presence of at least six inducing views lasting 200 msec each, in each trial of all conditions, we restricted the statistical analysis to these six views. The effect of the number of inducing views on the brain activity following their presentation will be addressed later.

Brain magnetic field strength changed significantly [$F(2.04,24.50) = 40.49$; $p < .0001$] with the display of each successive view (see Figure 2). The largest magnetic response was evoked by the first view and observed during the beginning of the second view display (see P200m in Figure 3). Then, possibly due to a habituation process, the amplitude of the brain response decreased slowly with each inducing view. Field strength varied significantly with topography [$F(2.78,33.40) = 8.89$; $p < .0001$]. Moreover, this topography changed significantly [$F(6.41,76.91) = 3.54$; $p = .003$] during the display of the six inducing views with the course of processing of the induced motion.

There was an overall tendency [$F(1,12) = 4.73$; $p = .05$], during the six inducing views, for root mean squared (RMS) field strength to be larger in the body ($M = 21.86$; $SD = 3.08$) rather than the picture condi-

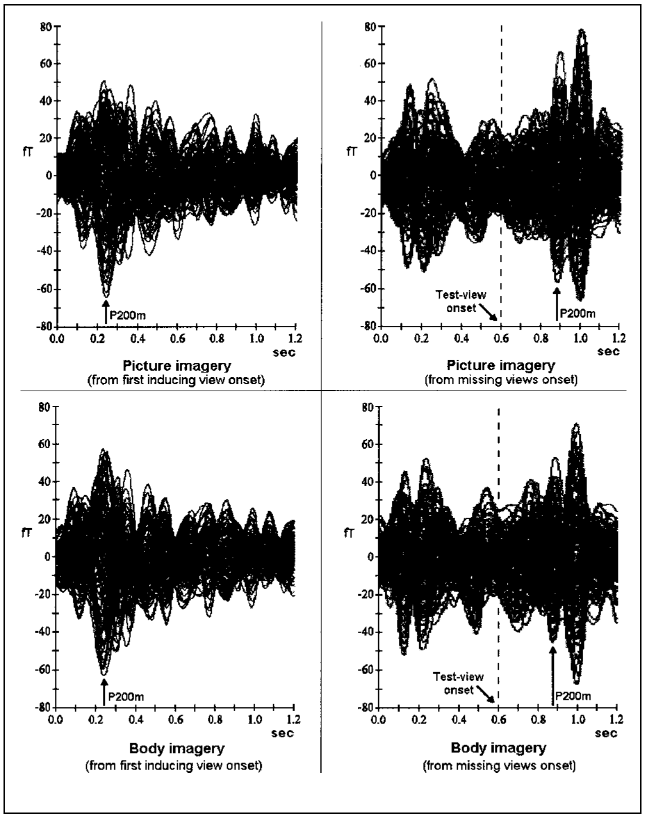

**Figure 3.** Grand-average evoked fields, over 13 subjects, for the six inducing views (left panels) and from missing views onset (right panels) for both mental imagery conditions. The arrows indicate the P200m component time-locked to the first inducing view and the final test-view.

tion ($M = 20.89$; $SD = 2.56$), but with similar spatial distribution [$F(4.80,57.64) = 1.39$; $p > .20$; *ns*].

## Motion Extrapolation

The image sequence was followed by three missing views during which the subjects continued to imagine either the picture or his/her body tilting, on the basis of the motion implied by the inducing views.

The ANOVA showed that the field strength varied with the three missing views [$F(1.61,19.33) = 10.41$; $p = .002$] and with topography [$F(3.55,42.63) = 6.73$; $p < .0001$]. Moreover, the topography of the field strength tended to change along the missing views [$F(6.95,83.45) = 2.04$; $p = .06$]. No main effect of imagery condition was detected [$F(1,12) < 1$; *ns*].

Afterward, the subjects judged if a proposed final orientation fell appropriately along the course of the previously implied motion.

## Processing of Static Spatial Orientation Information

We conducted a careful analysis of the response evoked by the first inducing view and the final test-view (cf. Figures 3 and 4). In both cases, the subjects needed to process the spatial orientation characteristics of the stimulus but for two different purposes. Processing of the first inducing view followed a mental rehearsal of the tilt displayed in the initial view (direction cue). This mental rehearsal occurred during the 3-sec pre-trigger time and foreshadowed a rotation of the view, whereas processing of the test-view followed a mental extrapolation of the implied motion (cf. Figure 1).

Visual inspection of field spatial distribution showed a similar activity peaking at the 240-msec postonset first inducing view and at the 284-msec postonset test-view (see Figures 3 and 4). This difference in P200m (see Discussion) peak maxima latency turned out to be significant [$F(1,12) = 12.44$; $p = .004$]. ANOVA on brain field strength for these peak activities showed a tendency [$F(1,12) = 3.57$; $p = .083$] for larger field strength following the first inducing view ($M = 47.52$; $SD = 29.90$) as compared to the test-view ($M = 41.04$; $SD = 23.05$). Although an ANOVA on reaction times to the test-view showed significantly [$F(1,12) = 12.03$, $p = .005$] greater values for the "body tilt" ($M = 1.27$; $SD = .38$ sec) than the "picture tilt" imagery ($M = 1.18$; $SD = .38$ sec), imagery conditions did not affect the P200m field strength [$F(1,12) < 1$; *ns*]. However, there was a significant effect of topography [$F(3.33,39.97) = 4.69$; $p = .005$] and a marginally significant interaction among topography, imagery condition, and stimulus type [$F(4.7,56.37) = 2.09$; $p = .085$] on the P200m field strength. The latter interaction is illustrated in Figure 4 by a higher density of outgoing magnetic fields (as indicated by the color blue) in the right-parietal region for the first inducing view as compared to the test-view, and increased field strength in the picture imagery condition as compared to the body imagery for the test-view.

Interestingly, it should be noted that the absence of any interaction between the stimulus type and topography [$F(5.30,63.59) = 1.31$; $p > .25$; *ns*] suggests that the P200m evoked by the first inducing view and the test-view may reflect a similar underlying functional activity, i.e., processing of the spatial orientation content of a static view. Particular attention was paid to the P200m field evoked by the test-view in order to examine if it might be modulated by RM.

## Representational Momentum Effect

The ANOVA showed a significant [$F(2,24) = 18.80$, $p < .0001$] decrease of reaction times to the test-view when more inducing views were shown (cf. Table 2), which did not differ with imagery conditions [$F(2,24) < 1$; *ns*]. RMS field strength of P200m to the test-view tended to increase with inducing views number (cf. Table 2), although not significantly [$F(1.64,19.67) = 2.52$; $p = .11$].

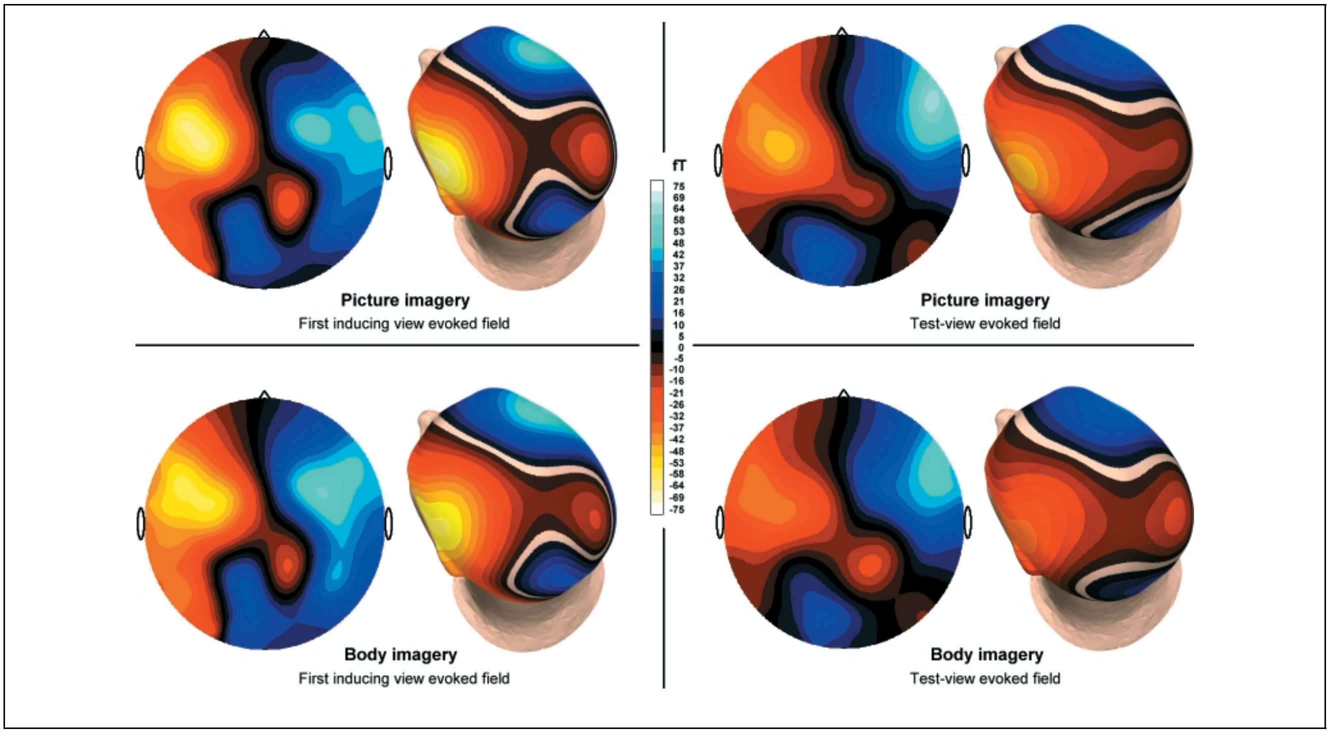

**Figure 4.** 2-D and 3-D maps of the P200m field maxima indicated in Figure 3. Outgoing magnetic fields are indicated by blue, whereas incoming fields are indicated by red.

Careful analysis of recognition performance at the test-view was conducted in order to test the presence of an RM effect. Analysis of hits (correctly identified test-views) and false alarms (backward and forward tilted test-views erroneously accepted as correct) was conducted carefully. The average rate of false alarms was .61 (*SD* = .20). Due to his high rate of false alarms (*M* = .98), the data of one subject were excluded from the analysis of the RM effect.

The ANOVA on average hits for the test-view showed no effect of increasing the inducing views number when the test-view was the correct one [$F(2,22) < 1$; *ns*], although this was accompanied by a decrease of reaction times [$F(2,22) = 6.21, p = .007$]. However, there was a significant [$F(2,22) = 13.21, p = .0001$] interaction (see Table 3) between the inducing views and the two types of distracting test-views on average hit, but not on reaction times [$F(2,22) < 1$; *ns*]. More precisely, the greater the number of inducing views, the more readily subjects accepted the forward tilted test-view as correct (decreasing hit = increasing false alarm) and they rejected the backward tilted test-view.

**Table 2**. Mean Reaction Time and RMS Field Strength (*SD* Between Parentheses) of the P200m Evoked Field Maxima Subsequent to the Test-View

| *Inducing Views (n)* | *Reaction Time (sec)* | *RMS Field Strength (fT)* |
|---|---|---|
| 6 | 1.26 (.38) | 52.44 (52.19) |
| 7 | 1.23 (.38) | 65.81 (56.76) |
| 8 | 1.19 (.37) | 68.01 (59.79) |

Closer inspection of Figure 1 as well as of Figure 5 will help us to understand this effect. When the inducing sequence contains six views, the last view has not yet crossed the horizon 0° level (given the starting view at −45°, and a rotation of 7.5° for each view, the last inducing view is at −7.5°, and the correct test-view expected at +22.5°) and subjects tend to accept a backward tilted test-view (15°) as correct, as if there was a slow down of the imagined rotation during the missing views (as symbolized by the magnet in the upper row of Figure 5). In Figure 5, the correct final orientation is illustrated with dashed line. On the other hand, after eight inducing views, the last inducing view has crossed the horizon 0° level and is at +7.5°, (correct test-view at +37.5°) and the subjects tend to accept a forward tilted test-view (45°) as correct, as if there was a speed up of the imagined rotation during the missing views (lower row in Figure 5). The seven inducing views sequence led to the more accurate answers to the test-view. The meaning of these results in terms of representational momentum will be discussed in the next section.

Interestingly, when testing for an imagery condition effect on RM (cf. Table 4), it appears that although the RM dynamics is the same for both imagery conditions, when answering to correct [$F(2,22) < 1$; *ns*)] or back-

**Table 3**. Mean Hit Rate (*SD* Between Parentheses) for Each Type of Test-View as a Function of Number of Inducing Views

| | | *Distractors* | |
|---|---|---|---|
| *Inducing Views (n)* | *Correct Test View* | *Backward Test View* | *Forward Test View* |
| 6 | .66 (.25) | .39 (.24) | .54 (.32) |
| 7 | .74 (.17) | .49 (.30) | .32 (.25) |
| 8 | .63 (.25) | .57 (.32) | .24 (.16) |
| Mean | .68 (.24) | .48 (.30) | .37 (.28) |

A "Hit" for the Correct Test-View Means "Correct Identification" of the Expected Test-View, Whereas a "Hit" for the Distractors Means "Correct Rejection." False Alarms = 1−Hit Rate for Distractors.

ward tilted test-views [$F(2,22) = 1.27$; $p > .10$; *ns*)], it differs significantly [$F(2,22) = 3.5$; $p = .048$] for forward tilted test-views. More precisely, subjects are significantly [$F(1,11) = 4.94$; $p = .048$] less biased (i.e., more hits) toward accepting forward tilts as correct in body imagery as compared to picture imagery. This difference is even greater [$F(1,11) = 8.8$; $p = .013$] when the last inducing view has not yet crossed the horizon 0° (cf. .61 vs. .46 in Table 4: forward test-view).

In order to reveal the brain dynamics of the RM effect, an ANOVA on the brain magnetic activity was conducted for trials with contrasted conditions. Accordingly, the data analysis was restricted to P200m responses evoked by the test-view for trials including either six or eight inducing views. Three "response types" were considered: (a) correct identification of the test-view (cf. .66 and .63 in Table 3), (b) trials showing an RM effect (lowest hit values for distractors in Table 3; cf. .39 and .24), and (c) trials running against the RM effect and for which there was a correct rejection of the test-view (highest hit values for distractors in Table 3; cf. .57 and .54). Given that both imagery conditions showed a similar RM effect (equivalent low hit values for distractors in Table 4; cf. .41 and .23 vs. .38 and .25 for picture vs. body imagery, respectively), we grouped their data together in order to test

**Figure 5.** Representational momentum effect: Depending on the number of inducing views, during the subsequent missing views where the previously implied motion is to be extrapolated, there is either a *slow down* (upper panels), or a *speed up* of the imagined rotation (lower panels), which induces false alarms. That is, subjects accept as correct either backward tilted views or forward tilted views after six or eight inducing views, respectively, instead of the correct view (in dashed lines).

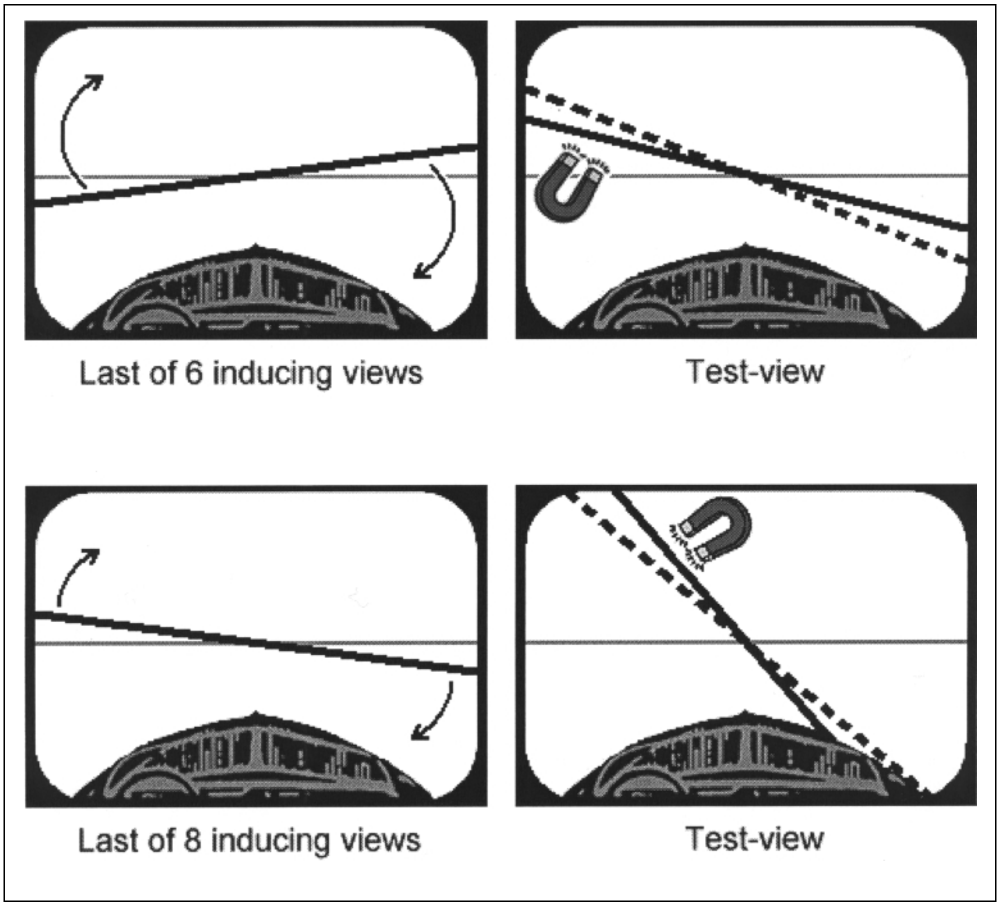

**Table 4**. Same as Table 3 but for Each Mental Imagery Condition

| | | | *Distractors* | | | |
|---|---|---|---|---|---|---|
| | *Correct Test View* | | *Backward Test View* | | *Forward Test View* | |
| *Inducing Views (n)* | *Picture* | *Body* | *Picture* | *Body* | *Picture* | *Body* |
| 6 | .67 (.26) | .65 (.25) | .41 (.23) | .38 (.24) | .46 (.32) | .61 (.30) |
| 7 | .75 (.20) | .73 (.15) | .46 (.32) | .52 (.28) | .30 (.24) | .35 (.26) |
| 8 | .63 (.28) | .63 (.23) | .55 (.32) | .59 (.31) | .23 (.15) | .25 (.17) |
| Mean | .68 (.25) | .67 (.22) | .47 (.30) | .50 (.29) | .33 (.26) | .40 (.29) |

for a topographical signature of RM at the brain field strength level. Maps of the average brain magnetic activity at the peak of the P200m evoked field to the test-view for each of these conditions are displayed in Figure 6.

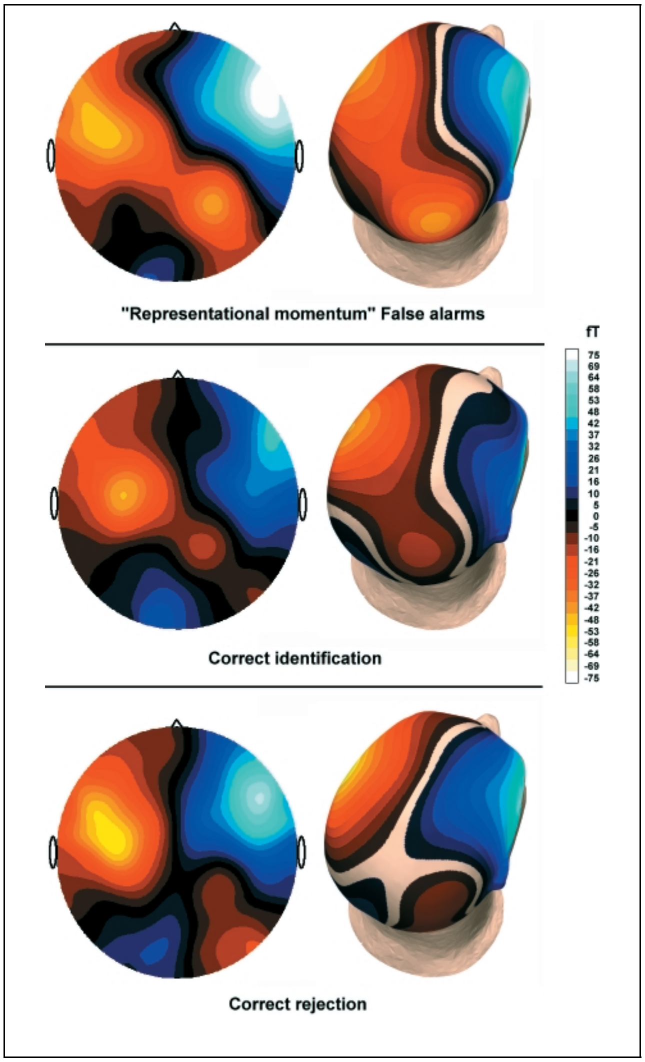

**Figure 6.** 2-D and 3-D maps of the grand-average P200m field maxima time-locked to the test-view for trials over 12 subjects leading to either false alarms indicative of a representational momentum effect, correct identification of the test-view, or correct rejection of distracting test-views. Outgoing magnetic fields are indicated by blue, whereas incoming fields are indicated by red.

An ANOVA on the RMS fT values for P200m maxima revealed a marginally significant difference among the three "response types" [$F(1.21,13.27) = 4.34; p = .051$]. Interestingly, the representational momentum effect led to a significantly greater field strength as compared to the trials leading to correct identification of the test-view [$F(1,11) = 9.72; p = .01$], but not to its correct rejection [$F(1,11) < 1$; *ns*]. Although very similar in terms of field direction (see Figure 6), the spatial distribution of field strength tended to be different for RM and correct identification trials [$F(4.88,53.71) = 2.12; p = .079$]. As illustrated in Figure 6, RM trials evoked increased magnetic activity in the fronto-lateral regions bilaterally and in the right superior-parietal region, as compared to the correct identification of the test-view. More precisely, this right hemisphere lateralization of RM trials in the spatial distribution of field strength was significant [$F(3.22,35.43) = 3.12; p = .035$].

## DISCUSSION

In this study, reaction time as well as brain magnetic field strength and latency were used as markers of neurocognitive processing. It is known that response times increase with task difficulty and engagement of additional processing resources (Luce, 1986), as revealed by the pioneering work of Donders (1868). Similarly, Gevins et al. (1996) showed that the amplitude of brain potentials (the EEG counterpart of MEG field strength) increases with task demand and additional processing. In the latter case, the involvement of extra brain regions to solve the task may accompany an increase in reaction times. Modulation of spatial orientation processing by mental imagery (cognitive set and representational momentum) was observed via those markers.

### Cognitive Set (Body vs. Picture Imagery)

Mental imagery instructions were used to drive perceptual interpretation of the visual input by focusing on either the visual scene orientation (picture imagery) or the body orientation relative to the latter (body imagery). The body imagery condition requires further processing of the visual input together with a reallocation of attention from vision to proprioception. As a consequence, body imagery requires more working memory resources as compared to the picture imagery. This difference was indeed reflected in both the reaction times and the brain magnetic field strength. It took more time for the subjects to imagine themselves being tilted relative to horizon, before any induced motion, than to observe the tilted horizon per se and make a perceptual decision. This difference was paralleled by a late CMV component of larger amplitude (≈ 17%) in the "body tilt" rather than "picture tilt" imagery condition, centered in the right centro-parietal region (≈ 30% larger). This CMV difference reflects differences in preparatory processes (Deecke, 1996) and is sensitive to working memory load (Gevins et al., 1996). Recent fMRI studies showed that performance during mental-rotation tasks was related to activity in the right-precentral gyrus (Tagaris et al., 1997) and the postcentral gyrus (Cohen et al., 1996). Therefore, we may hypothesize that the subjects anticipated the rotation to be induced by a forthcoming view sequence with the help of mental-rotation processes.

Interestingly, the effects of imagery on neuromagnetic field strength evoked by the inducing views and test-view were only marginal. So, the greatest mental imagery effect on brain field strength occurred when there was a stable unstructured input to the brain. This is during the pre-trigger period preceding the first inducing view when a random pixels view was displayed for 3 sec. Accordingly, the presence of structured visual input during the inducing views and test-view display may have reduced the amplitude of the imagery effect on field strength, due to the overriding of cognition by the spatial orientation processing of the visual input (Amorim, Loomis, & Fukusima, 1998). Noteworthy, no imagery effect emerged during the extrapolation period corresponding to the display of three different ramdom pixels views, possibly because the latter induced visually a random motion of pixels that acted also as an overriding visual input. Another evidence of the overriding of the visual input is the fact that, in the picture imagery condition, it takes longer to set mentally into a new orientation when the preceding trial ended with a tilt in the opposite direction (e.g., initial view is tilted CW whereas the preceding test-view was tilted CCW) rather than in the same direction (e.g., trial ending with a CW tilt followed by a trial starting with a CW tilt). No such effect was found in the body imagery condition where attention is redirected toward proprioception.

Finally, the similar spatial distribution of the brain magnetic fields in both imagery conditions is no surprise because the visual input was the same, only its cognitive interpretation varied via differential attention allocation. Consequently, it is the field strength rather than its spatial distribution that was modulated by mental imagery instructions. Otherwise, a difference in stimuli, e.g., when comparing mental rotation of objects vs. hands (Kosslyn et al., 1998), would have created artefactual differences in the spatial distribution of neuromagnetic fields.

## Processing of Static Spatial Orientation Information

Careful examination of the spatial distribution of fields evoked by both the first inducing view and the test-view indicated that the P200m component was a marker for the processing of the spatial orientation information. The peak latency of these P200m components was, respectively, 240 and 284 msec poststimulus onset, with fields located in the frontal and parietal regions bilaterally. Those fields may well belong to the family of longer-latency frontal P200 attention effects (Mangun & Hillyard, 1996). Their difference of latency might reflect the presence of additional processing for the test-view due to the comparison between the extrapolated and the current final spatial orientation. In contrast, the first inducing view showed more parietal activity than the test-view. Remember that this view belongs to a sequence of views inducing visual motion, and that its corresponding evoked field (P200m) occurred during the display of the second view. Therefore, the additional parietal activity might reflect an early integration of the spatial orientation difference between the first two views, which necessitates extra processing. The spatial organization of brain activity that we observed fits well with the literature on working memory. The bilateral coactivation of the inferior-parietal cortex and the dorsolateral-prefrontal cortex is frequently observed in working-memory tasks (Klingberg, O'Sullivan, & Roland, 1997). The large lateral-frontal activity that we observed reflects the fact that in human cortex, multiple, functionally distinct, prefrontal regions participate in working memory (Courtney, Ungerleider, Keil, & Haxby, 1997; Petrides, Alivisators, Evans, & Meyer, 1993). In general, top-down perceptual and imagery processing, such as in the perceptual-interpretation task we devised, is characterized by frontal, parietal, and anterior cingulate regions (Cabeza & Nyberg, 1997). Interestingly, examination of both behavioral and MEG data revealed that mental extrapolation of an implied motion is facilitated by increasing the amount of information available in the preceding inducing stimuli. Actually, the larger the number of inducing views, the greater the P200m field strength tended to be and the shorter the reaction time to the test-view.

## Representational Momentum

Following the literature on RM, we expected that the decision on the test-view would be biased toward false alarms for test-views rotated forward in the direction of the implied rotation (Freyd, 1987). On the other hand, some RM data suggest that, under special circumstances (e.g., representational friction or gravity), the RM dynamics may be biased in the opposite direction of the implied motion (Hubbard, 1995). Interestingly, our data suggest a combination of both effects relative to rotational equilibrium. The initial orientation of the inducing views was always a 45° tilt either clockwise or counterclockwise. When the missing views started before the sea panorama reached visual horizontal (cf. Figures 1 and 5), the subjects tended to choose the test-views oriented backward relative to the expected orientation given the motion implied in the inducing views. On the contrary, if the last inducing view had already crossed horizontal, the subjects accepted the test-views oriented forward relative to the correct view. This suggests that the mental representation of rotational dynamics mimics the physics of a seesaw, i.e., the role of gravity in rotational equilibrium. Implied gravity accelerates or decelerates the implied motion depending on whether the last view of the sea horizon has or not crossed visual horizontal yet, which corresponds to rotational equilibrium. Most interesting, the subjects are less biased toward accepting forward tilts as correct in body imagery as compared to picture imagery. This difference is even greater when the last inducing view has not yet crossed the horizon 0°. Probably due to the implied mass (Hubbard, 1995) of their virtual body, the subjects are reluctant to accept forward shifts when extrapolating the body rather than picture motion.

When examining the neural correlates of trials leading to an RM effect, we found evoked brain magnetic fields with a spatial distribution different from those leading to correct rejection or correct identification of the expected test-view. Large lateral frontal activity was present in the three response-type trials. However, RM trials showed more activity in a region located around the right centro-parietal region. Interestingly, this region is the same as that activated during the mental rehearsal period preceding the first inducing view, during which the subjects anticipated the rotation of the forthcoming views, possibly with the help of mental rotation processes. Therefore, our results are compatible with the idea of a communality of neural structures and processes for the control of both RM and mental rotation. Accordingly, we may hypothesize that representational momentum is a further processing stage that builds on structures devoted to visual motion perception and imagination (mental rotation). In addition, our finding of a right hemisphere lateralization of P200m spatial distribution for RM trials is compatible with results from the visual half-field RM experiments showing larger memory shifts for targets falling in the left visual field, i.e., right hemisphere (White, Minor, Merrell, & Smith, 1993).

Finally, brain field strength was stronger following test-views inducing either RM or running against RM, as compared to those leading to correct identification. Accordingly, increased brain magnetic activity may reflect early (P200m) and non-voluntary detection of an incongruity between the expected and the displayed test-view. In effect, although the test-view was accepted as correct for RM trials, brain activity was larger than in correct identification trials, and not different from correct rejection of test-views running against a RM effect. This last result fits well with the hypothesis stated by Hubbard (1998) that, in order to provide selective advantage to a predator or a prey that could anticipate and extrapolate the effects of physical principles on stimuli, this extrapolation process should occur automatically and best be accomplished by nonconscious processes.

## METHODS

### Subjects

Thirteen subjects volunteered to participate in the experiment (six right-handed men, two left-handed men, and five right-handed women) between 19 and 33 years of age. All subjects had normal or corrected-to-normal (contact lens) vision and were naive with regard to the purpose of the experiment, as well as paid for their participation. Handedness was tested using a modified Oldfield (1971) questionnaire.

### Material

The experiment took place in an electromagnetically shielded room under very dim lighting conditions. The visual stimulation was displayed onto a screen via a mirror reflecting 640 × 480 pixels images sent by a projector connected to a personal computer. The present experiment was generated and monitored via ERTS-VIPL (BeriSoft Coop.), a PC-compatible software package allowing development and performance of psychological experiments (Beringer, 1994a, 1994b). The subjects sat comfortably in front of the display. The screen was placed 2 m away from the subject at eye-level. In order to eliminate environmental cues, the visual field was restricted towards the visual stimuli via a rectangular optical tunnel. Responses were recorded via two hand-pedals. Text instructions (written in white characters) as well as gray-level colored stimuli were displayed against a dark background.

### Procedure

An example of stimuli sequence is displayed in Figure 1. Subjects initiated each trial by pressing a hand-pedal.

A fixation point at the center of a circle of 11° of visual angle was displayed for 3 sec against a random pattern. The instructions "body tilt" or "picture tilt" were displayed around the fixation point, only on this "announcement" stimulus, in order to remind the subject of the condition of the current trial. The large circle and the fixation point were displayed on each image in order to cover the area centralis of the retina and maintain a stable image on the fovea. Then, an initial view (27 × 19° of visual angle) representing a tilted sea horizon (45° CW or CCW) and acting like a "direction cue" stayed on the screen until the subject pressed a pedal to start the sequence of views. The task of the subject during the initial view was to imagine either being tilted relative to the horizon (body tilt) or to observe the latter per se (picture tilt). This view was replaced by a random pattern for 3 sec, after the subject pushed a hand-pedal, so that the cortical activity evoked by the hand movement returned to a baseline. Then, a sequence of rotating horizon views started during which the subject imagined either his/her "body motion" corresponding to the rotation of the horizon (body tilt), or focused attention on the "picture rotation" itself (picture tilt). The sequence of inducing views varied from six to eight views. On each horizon view displayed to the subject, the prow of the boat on which he/she was supposed to sit was overlaid at the bottom of the picture. The axis of rotation of the horizon picture was centered on the top of the boat prow. The amount of rotation of the horizon line after each inducing view was 7.5°. Given that each view was displayed for 200 msec, the implied velocity of the view rotation was 37.5°/sec. The inducing views sequence ended with a series of three different random patterns, and a test-view. The three random patterns were generated by randomization of the pixels of the three missing views between the inducing and test-views (see Figure 1). The test-view was followed by its randomized pixels version displayed for 2.8 sec. Then, the next trial started automatically. The subject was instructed to indicate if the (either "body" or "picture") orientation referred by the test-view was the one that would be expected given that either his/her body (according to the horizon) or the picture motion was to be imagined during the missing views, according to the momentum implied by the inducing views. The subject pushed the right pedal for "Yes" and the left one for "No." If the allowed response time (3 sec from test-view onset) was exceeded, a "wake-up" message was displayed.

Unknown to the subject, the test-view could be either the correct one (that is $3 \times 7.5 = 22.5°$ farther away from the last inducing view), or a distractor oriented either −7.5° (backward tilt) or 7° (forward tilt) with respect to the correct view, i.e., either the immediately preceding or subsequent view. Accordingly, acceptance of the distracting views as correct or rejection of the correct test-view indicated a false alarm or a miss, respectively. For half of the motion picture sequences, the horizon rotation was in the clockwise direction and counterclockwise for the other half. The experiment consisted of three blocks of 108 trials, with 54 consecutive trials in each condition ("picture" vs. "body" tilt). A 5-min pause followed each block of trials. The trials included an equal number ($n = 18$) of sequences differing only by the number of inducing views.

Before the experiment started, there were 12 training trials (six per imagery condition) that were not included in the data processing.

## MEG Recording and Analysis

Brain magnetic activity was measured using the CTF™ 143 channels whole-scalp MEG equipment (Beisteiner, Vrba, & Deecke, 1998; Vrba et al., 1996), with a sample frequency of 250 Hz. The spatial distribution of the SQUID sensors all over the scalp is illustrated in Figure 7 in both two and three dimensions. The 3-D representation was obtained using a spherical projection of the 2-D map onto a realistic head model. All the system characteristics from hardware (sensing system and electronics) to software (data acquisition and analysis) are available from the CTF™ web site at http://www.ctf.com. The MEG system that we used is located at the Department of Neurology of the University Clinic of Neurology, Vienna, Austria.

MEG data were recorded over the entire course of stimulus presentation, broken into categories based on time intervals, and averaged within categories in order to perform statistics. Recordings were triggered by the onset of the first inducing view and ended either with the subjects answer to the test-view or 3-sec post test-view onset. Trials including eye blinks or eye movements were excluded on the basis of visual inspection of the MEG frontal channels. The 1000 msec preceding the trigger were used as a baseline for the subsequent MEG data filtered with a .5 to 10 Hz band pass. Field strength during pre-trigger time was further analyzed in order to test the presence of a CMV, i.e., the neuromagnetic counterpart of the Contingent Negative Variation slow-wave, reflecting anticipatory processes. Therefore, the 1000-msec pre-trigger period was filtered with a .25 to 10 Hz band pass. The first 250-msec time interval (i.e., from −1000 to −750 msec pre-trigger) served as a baseline, and the subsequent 400- to 1000-msec interval was taken into account for statistical analysis. More precisely, we divided this 600-msec time interval into three intervals corresponding to early (−600 to −400 msec pre-trigger time), middle (−400 to −200 msec), and late (−200 to 0 msec) CMV components (cf. Figure 2).

For the analysis of MEG data, which are magnetic third-order gradiometer values in femtoTesla (fT), we considered two additional within-subjects factors: to-

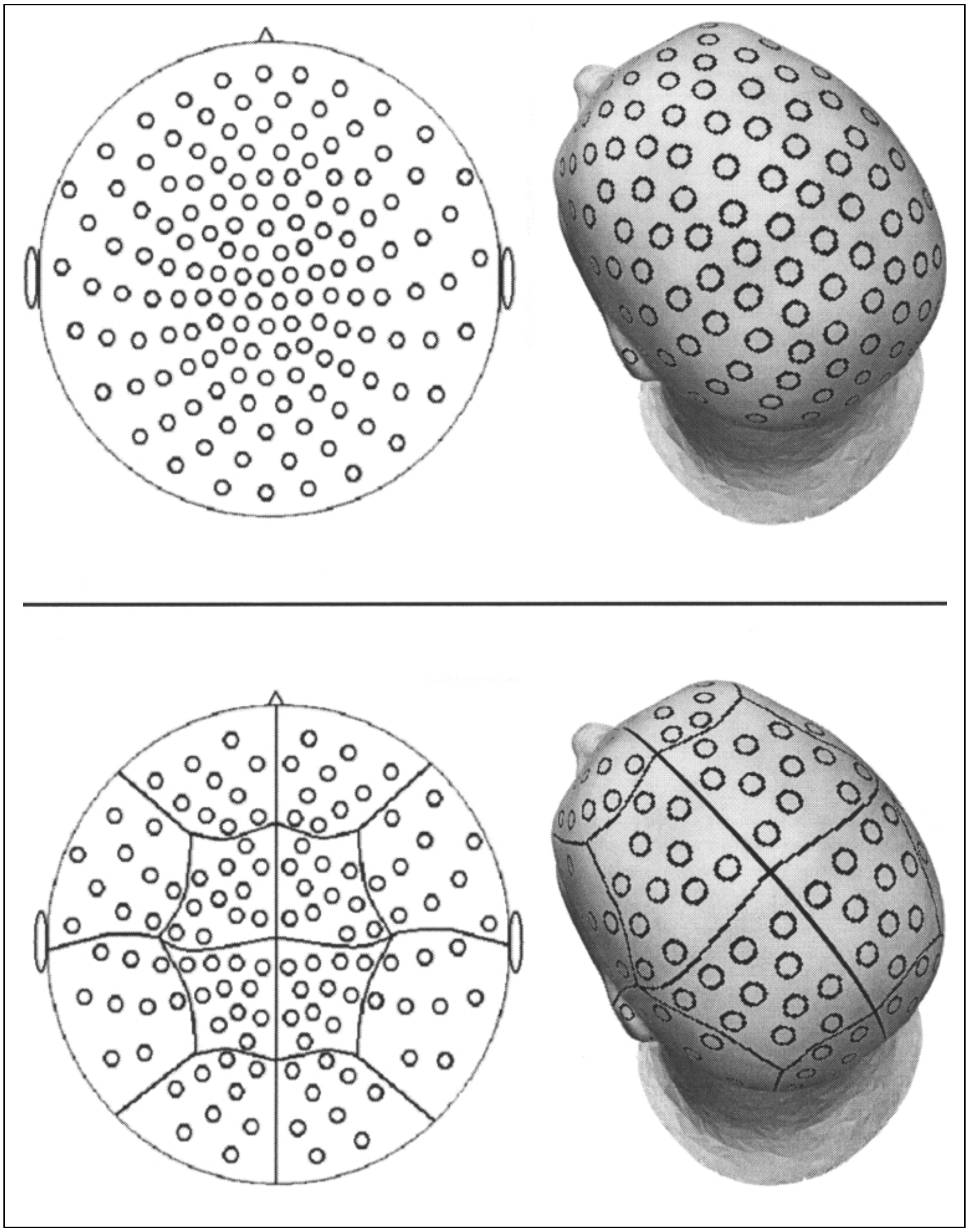

**Figure 7.** Upper panel: 2-D and 3-D projection of the approximate relative locations of the 143 MEG sensors, which we used to display the brain magnetic fields in Figures 4 and 6. Lower panel: MEG sensors isolated in order to build 12 contrasted brain regions for statistical analysis (topography factor) of averaged RMS field strength values over time intervals.

pography of the magnetic activity and time intervals. The level number of the latter factor varied depending on the hypotheses being tested. The topography factor was the result of a concatenation of the MEG sensors as illustrated in Figure 7, in order to isolate the activity at the brain region levels rather than to stick to each sensor separately. Some of the sensor data (typically those overlapping two or more "brain regions") were not used for building the 12 levels of this topography factor, in order to have clear-cut brain regions. Although the data at the sensor level are relevant when displaying measured fields in 2- or 3-D maps, brain regions allow more neurofunctional interpretation of the data. The isolated regions were prefrontal, fronto-lateral, precentral, superior-parietal, inferior-parietal, and occipital, for both the left and the right hemispheres.

The MEG signal averaged per time interval contained signed values that were RMS in order to get rid of the bias introduced by the fact that a magnetic field detected as coming out of the brain (positive fT values) must get back in (negative values). Accordingly, if RMS was not applied, the expected averaged brain activity would be zero! Therefore, this data transformation is commonly applied (Mecklinger et al., 1998; Kaneoke, Bundou, Koyama, Suzuki, & Kakigi, 1997).

The other within-subjects factors were mental imagery conditions ("picture-" vs. "body-tilt"), inducing views number (either 6, 7 or 8) and test-views (correct view vs. backward tilted vs. forward tilted). The behavioral dependent variables were response latencies and error rate.

The results of the repeated-measures analyses of variance (ANOVAs) on field strength are given with corrected degrees of freedom to control for the possible correlations among levels of repeated measures (sphericity assumption). This correction was done by multiplying the original degrees of freedom by the Greenhouse–Geisser epsilon (Vasey & Thayer, 1987; Greenhouse-Geisser, 1959) for all the effects with two or more degrees of freedom in the numerator, and the $p$ values were computed accordingly. Finally, it is noteworthy that even highly significant effects at the sensor level may be swept out by regional grouping of sensor data (topography factor) or when examining other main conditions (e.g., mental imagery factor). Therefore, marginally significant values ($p < .10$) are also reported as being tentatively suggestive of an effect.

## Acknowledgments

We thank Fred Lacloche for the preparation of the sea panorama stimuli, and Sreng Truong for the pixels randomization program, as well as John Morgan and two anonymous reviewers for their comments on a first draft of this paper. We also thank Bernard Renault and Stephen Kosslyn for their comments on the preliminary results of a pilot study. This work has been supported by a European Union post-doctoral Marie-Curie Fellowship to M.-A.A.

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