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FROM VISUAL MOTION PERCEPTION TO SPATIAL COGNITION
Study of behavior and brain activity

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FOREWORDS

Open your eyes! By simultaneously processing numerous visual cues, your brain allows you to locate yourself in the environment, recognize the surrounding objects and estimate their distance, identify people and anticipate their movements. Take a look to the left, turn your head and step forward: The visual signal rapidly changes on your retina, but the world appears stationary.

Visual motion is an amazing cue. Obviously, it gives us access to the movement of the surrounding objects, allowing us to anticipate their future position and interact with them efficiently: avoid a bicycle on the road, catch a ball, or pour tea into a cup without overflowing. Less obviously, visual motion also informs us about our own movements: the movement of our gaze in the visual scene, the movement of our body in space. Paradoxically, it is likely that the more accurately this information is processed, the more the motion sensation is suppressed, so the less we perceive it. Last but not least, visual motion also provides us with information about the 3-D layout of our environment. This can be easily realized when looking through a train window: the nearby elements of the landscape rush by us, while the more distant ones appear motionless. Those relative visual speeds are the cue revealing the underlying in-depth structure of the scene.

Since my PhD Thesis, my first interest was to understand by which processes the brain could extract depth information from visual motion, and how it could, from one same visual flow, distinguish between the motion related to the 3-D structure of the object and that related to its movement. To that end, I used stimuli devoid of shape and contour information and explored the brain regions involved in building 3-D shape information from visual motion only.

The apparent cross talk between visual motion and form information led me to question the possible interactions between the two visual features. Is there any evidence of the motion feature influencing the shape feature, or reciprocally? Using behavioural testing and brain imaging in the framework of different collaborations, I thus examined the relationships between motion and shape processing. This work has been conducted from 2001 to 2005 in the group of Jacques Droulez at the 'Laboratoire de Physiologie de la Perception et de l'Action' (LPPA), headed by Pr. Alain Berthoz; from 2006 to 2008, in the group of Jean Lorenceau at the 'Laboratoire de Neurosciences Cognitives & Imagerie Cérébrale' (LENA), headed by Dr. Line Garnero, and from 2009 to 2012, at the Brain and Spine Institute (ICM).

In 2012, I joined Laure Rondi-Reig's lab to explore new topics: cerebellum, navigation and memory, or how brain structures interact during self-motion to implement space cognition. I thus discovered that the cerebellum was not just a little pernicious structure aimed at masking the ventral surface of the visual cortex in fMRI and in turn I had a chance to convince my new lab partners that the visual cortex was not just a big fat structure intending to crush the cerebellum...

Given the various types of information associated with 'visual motion' in this document, I have tried to use specific words to disentangle the different possible meanings and better characterize the studied processes. In the following, I will thus specify 2D visual motion as a synonym for optic flow, which is the change of local contrasts on the retina due to relative movements between the eyeball and the visual scene or its elements. Moreover, I will distinguish this 2D component of the physical motion projected on the retina of the observer from the 3D motion perceived by the observer once the retinal signal has been decoded by the brain.

In the first part of this manuscript, I address how the brain reconstructs the 3D features of visual objects (3D motion and 3D shape) from the 2D visual motion projected on the retina. In this part, we consider static observers and make the assumption that visual motion is related to the surrounding visual objects only. To further isolate the activity related to the structure from motion process, we used impoverished visual stimuli providing structure information from motion inputs

only. We then studied the possible interactions arising between the different perceptive attributes extracted from this unique visual input, and further explored whether they could be mediated by stimulus-driven or task-related processing.

In a second part, I address more widely the question of feature integration and selection through some collaborative studies. In particular, I consider structure perception from the perspective of 'visual binding', and feature interactions from the perspective of object-based attention.

In the third part, I address the neural bases of spatial cognition and specifically how the cerebellum may contribute to process sensory inputs during navigation to disentangle self-motion information from external cues.

The last two parts shortly present the on-going projects in which I participate. They are organized in two topics: the electrophysiological investigation of cerebellum-forebrain coupling and the use of navigation tasks as a translational tool to explore cognitive deficits, with application in autistic spectrum disorders (ASD) and Alzheimer's disease.

GLOSSARY

MT: middle temporal area; area processing visual motion in monkeys, also called V5

hMT: human MT, also called V5 or hMT/V5

hMT+/V5+: stands for hMT/V5 along with its satellite areas also sensitive to visual motion

fMRI: functional Magnetic resonance Imaging

MEG: Magneto-Encephalography

ASD: Autistic Spectrum Disorder

3D MOTION AND 3D FORM FROM 2D MOTION

With one eye shut, depth perception is severely impaired and it proves difficult to determine which pen is the closest in the pencil pot for example. However, it is possible to gain depth information again just by moving one's head back and forth or left and right, or by rotating the pot in one's hand. This perception of the structure from motion has a twofold interest. First, shape information is extracted from a motion signal, which reveals a link between features often considered independent. Second, the process of extracting structure from motion also leads to 3D motion information, so that two distinct perceptual features –motion and form– are extracted from a unique sensory input, which is retinal speed distribution.

The extraction of 3D structure information from 2D motion has been theoretically described as a hierarchical process divided in two main stages (Hildreth and Koch, 1987):

- optic flow characterization, through the measurement of the retinal speeds and their gradients;
- recovery of the 3D layout of the scene, from a depth map relative to the observer to a 3D representation independent of the observer's viewpoint.

By studying motion and shape perception from retinal speed distribution, it becomes possible to disentangle these two stages of perception: the analysis of the 2D visual input on one hand, and the coding of the reconstructed perceptual attributes, namely 3D motion and shape, on the other hand.

The issue is to fit this theoretical model with a neurophysiological substrate. The human retina encodes spatial and temporal variations of luminance but does not provide an actual speed distribution. In V1, most motion-sensitive cells encode ambiguous speed directions, because only motion orthogonal to a contrast edge is extracted. In area MT/V5 however, cells are able to encode 2D motion information. In addition, it was shown in monkeys that, thanks to the specific organization of their receptive fields, some MT cells are selective for the orientation in depth of a surface defined through visual motion (Xiao et al., 1997). Those specificities thus make MT a likely candidate to implement the first stage of structure-from-motion extraction.

To study the fMRI activity induced by depth perception from visual motion cues, independently of any other static cue, we used random dot stimulation. With a random distribution on the screen, dot arrangement does not provide any structure or shape information as long as the view is static. Yet, the movement of each dot is computed as if they belonged to a 3D rigid surface oscillating in depth, so that the shape of the underlying surface can be recognized through the succession of views (see Figure 1).

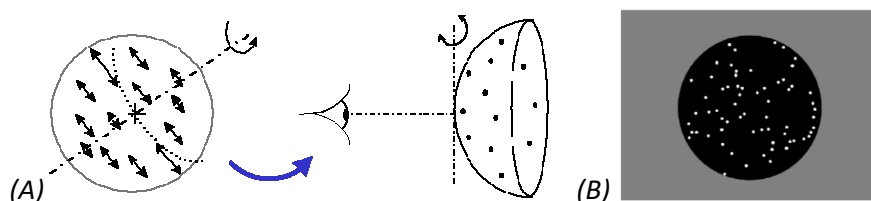


Figure 1. Distribution of speeds and 3D perception generated by this distribution (A). Snapshot of the random dot distribution on the screen (B).

In humans, functional brain imaging studies revealed a large 'visual motion' network of occipito-parietal and posterior temporal areas (including MT) sustaining the perception of coherent and/or structured motion (Braddick et al., 2000; Kriegeskorte et al., 2003; Murray et al., 2003; Orban et al., 1999; Paradis et al., 2000; Peuskens et al., 2004). Human electrophysiology further highlighted that perceiving objects defined by motion induced sequential activity, with early activation of the occipital visual cortex and later activation of the lateral occipital and temporal areas involved in shape recognition (Jiang et al., 2008).

The number of different visual areas highlighted by those studies raises questions about the specific role of each one in the analysis of those coherent motion stimuli. We hypothesize that part of those

regions are involved in the early processing of optic flow, while others contribute to the subjective perception of the object motion and form – both simultaneously available when perceiving structure from motion. Furthermore, it is also likely that some are involved in attentional and decisional processes related to the task performed by the observer. In the studies presented below, we used brain imaging and behavioral exploration to better understand the different processes and brain areas at stake when perceiving 3D motion and 3D form from 2D retinal motion.

Publication: Paradis AL, Droulez J, Cornilleau-Peres V, Poline JB (2008) Processing 3D form and 3D motion: Respective contributions of attention-based and stimulus-driven activity. Neuroimage, 43: 736-47 (attached in Annexes) <http://dx.doi.org/10.1016/j.neuroimage.2008.08.027>

The aim of this first study was to segregate the brain activity related to the perception of the 3D shape from that related to the perception of the 3D motion, while disentangling the analysis of the visual inputs from the influence of the attentional selection.

Protocol and results

Because we cannot just selectively suppress motion or shape information in the structure-from-motion stimulus to highlight the activity related to the processing of each attribute, we introduced independent variations of motion and shape along time. To further dissociate the activity related to the analysis of the visual transitions from the attention directed to the perceived attributes, we instructed the participants to alternately detect motion, shape or color changes. We thus disposed of two experimental factors (visual transitions and attentional selection through the task) to target the brain activity related to each perceptual attribute (see Figure 2).

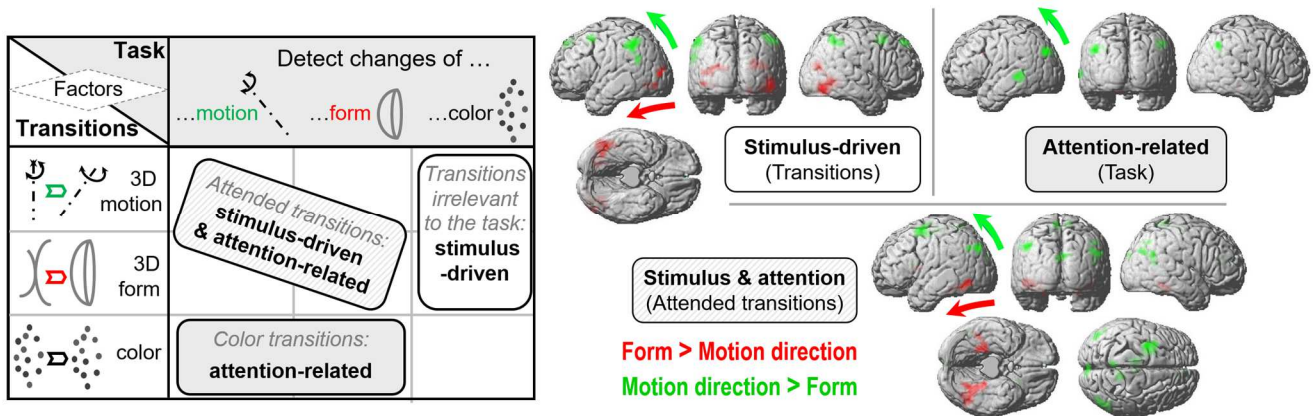


Figure 2. Experimental design (left) and main results (right). Adapted from Paradis et al., 2008.

Following the study by Corbetta et al. (Corbetta et al., 1990) with color, speed and shapes defined by contours, our assumption was that attention to the 3D perceptual attributes of an object would enhance the activity in the areas processing these attributes, and that these areas would be the same as those activated when passively presenting the perceptual changes, supposedly the above described 'visual motion' network.

As a first result, the segregation of activity between 3D motion and form very nicely fitted the classical dichotomy of the visual system into two pathways. Whatever the contrast (unattended transitions, task modulation only or attended transitions), 3D motion was associated with activity in the dorsal pathway and form with activity of the ventral pathway.

However, contrary to our initial expectations, the activity involving attention selection (contrasts 2 and 3 in Figure 2) was not just an enhanced version of the activity elicited by the unattended transitions (contrasts 1). In fact, the main foci of activity for each attribute did not overlap between the two contrasts (compare dotted and solid lines for each contrast). Furthermore, the observed activity was not restricted to the classical 'visual motion' network, especially for 3D motion and/or attended transitions. Thus, it seemed that paying attention to the 3D motion or form of the objects did not just consist in modulating the activity of areas otherwise involved in the automatic processing of those visual features.

Further analysis revealed that both the motion and form unattended transitions induced enhanced activity in the network classically associated with the perception of coherent visual motion (*Figure 3.A*), as well as possible decreased activity in the default mode network (Raichle et al., 2001) (*Figure 3.B*). In contrast, attended transitions induced little activity increase (*Figure 3.C*), but extended activity decrease in brain regions located downstream the above-mentioned network (*Figure 3.D*). Of note, this activity decrease appears in the ‘competing’ pathway compared to the attended attribute, i.e. decreased activity in the dorsal pathway for attended transitions of form (in red) and decreased activity in the ventral pathway for attended transitions of 3D motion (in green).

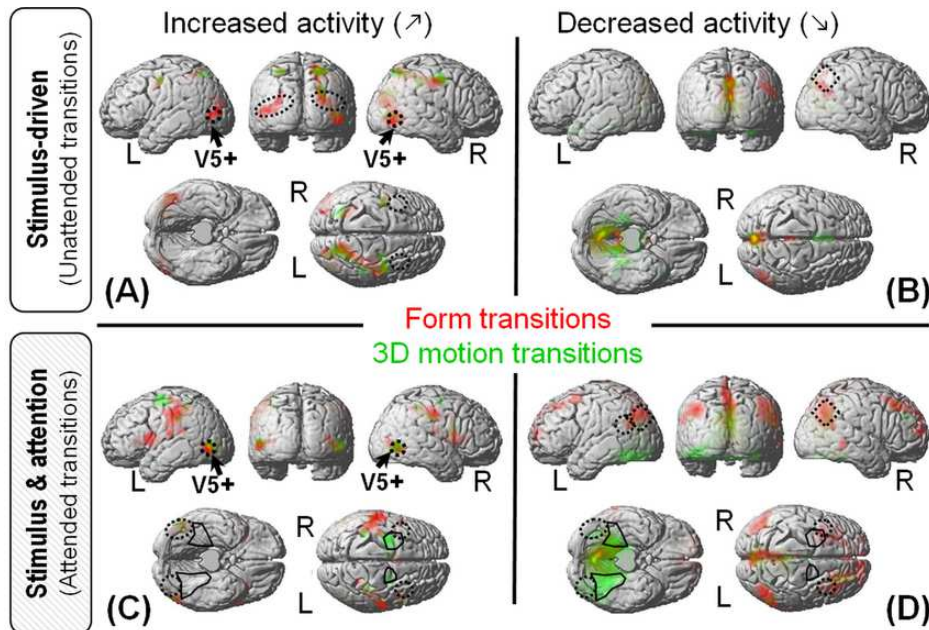


Figure 3. Activity with respect to a ‘low level baseline’ without 3D structure nor visual motion: increased/decrease activity (Left/right) for unattended /attended transitions (Top/Bottom). Figure from Paradis et al., 2008.

Discussion

In summary, the activity in the classical ‘visual motion’ network including MT/V5 and intraparietal areas appears enhanced by all –attended or unattended, 3D motion and form– transitions (see *Figure 3*) without significant selectivity for one perceptive feature compared to the other. Accordingly, this network likely sustains the analysis of the visual inputs (2D speed distribution) rather than the perception of 3D motion and form *per se*. In contrast, differential activity between 3D motion and form clearly highlights the segregation into two pathways: dorsal for 3D motion and ventral for form. However, this attribute-specific activity appears to depend on whether the feature is attended or not. Then, processing the 3D perceptual attribute may depend on different mechanisms –possibly excitatory versus inhibitory– depending on the task performed by the observer (automatic perception versus active detection). Although difficult to interpret if we do not distinguish 2D motion processing from 3D motion perception, those results are fully compatible with two stages of the computation and different effects of the attentional selection at each stage. Figure 4 illustrates a possible mechanism of attentional selection accounting for those results.

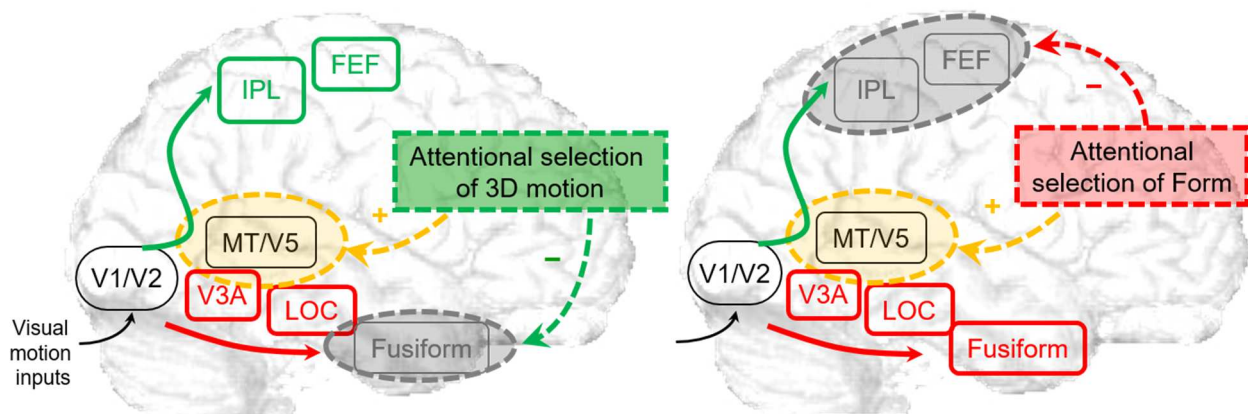


Figure 4. Proposed mechanism for the attentional selection of the 3D features: 3D motion (left) and form (right). Selection per se might arise through down modulation (left, -; right, -) in the pathway processing the concurrent feature (i.e. ventral areas for attention to 3D motion vs. dorsal areas for attention to form). Attention directed toward either feature however induces a non-specific enhancement (+) in MT/V5 likely helping to process the 2D visual input from which both features are extracted.

Note that the observers were never passive in this experiment. During the unattended transitions, they were in fact performing a visual task related to color. Although irrelevant and independent from motion processing, this task was still likely to orient subjects' attention toward the visual modality, and may have globally induced non-specific activity enhancement. To further characterize the activity of the regions found selective for 3D motion and form in different perceptual contexts, I now wish to present additional unpublished data recorded in actual passive viewing.

Additional unpublished data: 3D motion and form attributes in passive viewing

https://www.researchgate.net/publication/311809839_Specificity_of_the_responses_to_3D_motion_and_form_in_passive_viewing

In this experimental condition, I targeted the areas highlighted in the previous study (Figure 5A) and tested their response to changes of color, 3D motion or form viewed passively (Figure 5B). For the motion and form attributes in particular, I wished to check whether the activity evoked by unattended transitions (i.e. occurring during the color task: Figure 5A, **Unatt** and **Unatt**) was similar to the activity evoked by passively viewed transitions (Figure 5B, **F** and **M**).

In the occipito-temporal regions of the ventral pathway, there was significant activity related to passively viewed form transitions, consistent with the previously established selectivity of those regions (Figure 5A). In contrast, no significant activity was found in the dorsal regions whatever the modulated attribute (Figure 6B). This absence of significant activity could be due to a decrease of signal and statistical power in passive viewing compared to active conditions. In line with this, the two ventral areas V3A and LO keeping significant activity in passive viewing also presented greater activity than all other areas in the active conditions. However, the dorsal regions not only show reduced activity: most of them also appear to lose their selectivity for the 3D motion feature, and the activity of medial FEF and cuneus could even be suggestive of a selectivity for form in passive viewing conditions

Overall, these results suggest that the dorsal areas considered here are selective for 3D motion and activated by 3D motion transitions in a task context only. This is consistent with the dorsal pathway associated with perception for action (Goodale and Milner, 1992): dorsal areas would be less active in the absence of a task requiring action after perception. It is also reminiscent of how task 'usefulness' may affect perception in transparent motion stimuli (Chopin and Mamassian, 2011). Thus, we can hypothesize that dorsal areas may support perceptual decision about motion depending on the task. This however

questions whether there is an automatic processing of objects' 3D motion or whether accessing this feature systematically requires attention.

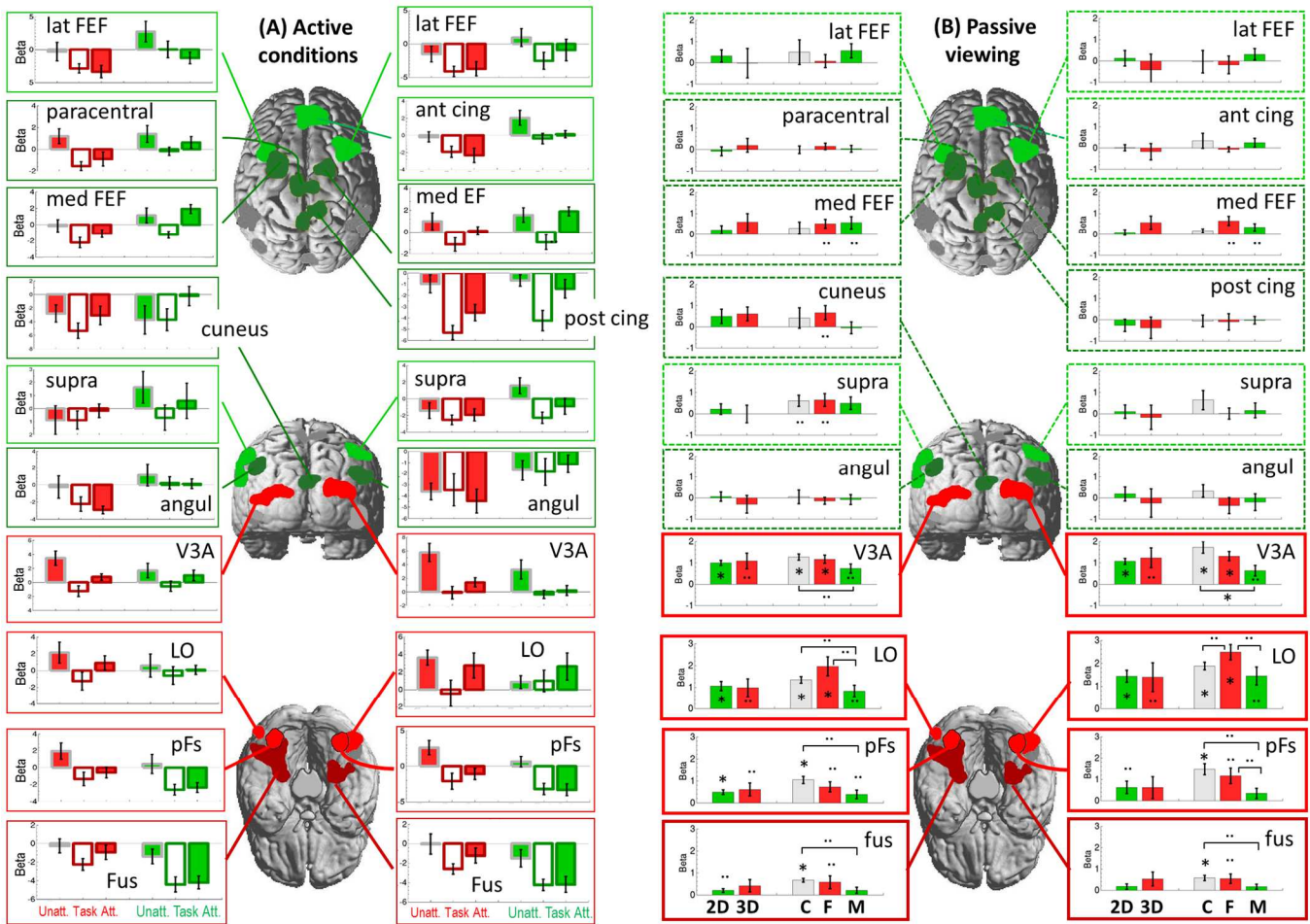


Figure 5. Compared pattern of activity in active and passive viewing conditions. Regions of interest are defined and colored depending on their activity in the active conditions reported in Paradis et al., 2008. Green ROI were more activated by 3D motion than form in either unattended (•) or attended (•) transitions. Red ROI were more activated by form than 3D motion in unattended (•) or attended (•) transitions. For each ROI, the activity profile plots the mean amplitude of response (SPM beta \pm one standard error) to each type of transition. **(A)** Activity observed in the active conditions for form/3D-motion transitions during the color task (Unatt./Unatt); for color transitions during the form/3D-motion task (Task/Task); for form/3D-motion transitions in the form/3D-motion task (Att/Att). **(B)** Activity induced by passively viewed transitions of 2D motion (2D), from 2D motion to a 3D object (3D), Color (C), Form (F) and 3D motion (M).

* $p < 0.05$, corrected for the number of tested regions; double dots: uncorrected $p < 0.05$.

Interaction between form and motion attributes in 3D structure-from-motion perception

Publication: Miskiewicz A, Buffat S, Paradis A-L & Lorenceau J (2008) Shape and motion interactions at perceptual and attentional levels during processing of structure from motion stimuli. Journal of Vision, 8(16):17, 1-14 <http://dx.doi.org/10.1167/8.16.17> (attached in Annexes)

This study was part of Agnieszka Miskiewicz' PhD work. A Miskiewicz was co-supervised with Jean Lorenceau (ICM), in the framework of a collaboration with S. Buffat (IRBA, ex-IMASSA).

With 3D structure defined from motion, the 3D motion and form attributes are both extracted from the retinal distribution speed. We then wondered whether these attributes could actually be processed independently or whether their common source could induce interaction between them.

Protocol and results

To answer this question, we used a rapid visual serial presentation (RSVP) protocol (Figure 6). After being presented a rapid sequence of three 3D-from-motion stimuli, participants were asked to report the number of times they had perceived a specific form or a specific motion direction. To perform this task, the participants not only have to perceive and identify the form and/or motion direction (i.e. type) of the stimulus, they also have to attribute a 'token' to their perceptions in order to individuate and count their occurrences (Kahneman et al., 1992; Kanwisher, 2001, 1987). This protocol thus involves two stages of processing at least, likely related to feature perception on one hand and episodic memory on the other hand. To reveal the possible interaction between motion and form at the two stages, we evaluated the observers' performance in both motion- and form-related tasks, depending on whether the C1 and C2 items (see Figure 6) were different or shared similar motion and/or shape features. The overall percentage of correct responses was used to evaluate type identification, while the repetition effect was assumed to evaluate token attribution.

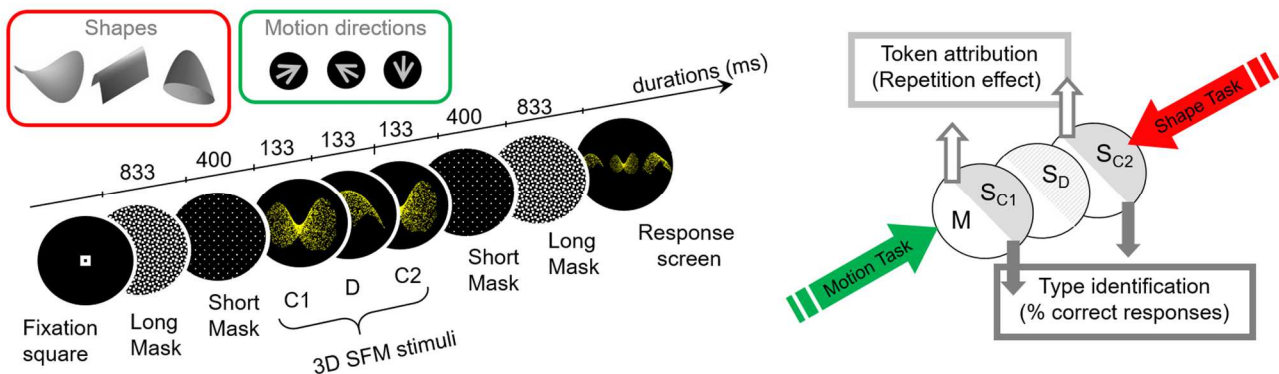


Figure 6. RSVP protocol (left) and working hypotheses (right). Depending on the task, observers had to report either the shapes (S) or the motion directions (M) of the three structure-from-motion (SFM) stimuli. C1 and C2 could have identical or different features (repeated vs. non repeated condition with respect to the feature). D was always different from C1 and C2. Correct responses corresponded to both C1 and C2 being reported correctly, i.e. feature reported twice if repeated or C1 and C2 features reported once only if different. D could be reported once or omitted. The repetition effect is the difference of correct responses between repeated and non-repeated conditions. Adapted from Miskiewicz et al., 2008.

Overall, performances were higher when the task concerned the motion direction rather than the form. For the motion task, performances were poorer when motion direction was repeated, revealing repetition blindness (Figure 7A). In contrast, performances were increased when the form, irrelevant to the task, was repeated, although the rate of repetition blindness to motion direction was not modified (See Figure 7B).

For the form-related task, we did not find any repetition blindness at the group level, i.e. no effect of repeating the form on the subject's ability to report the perceived shapes and their number of occurrences (Figure 7C). In addition, repeating the motion direction, irrelevant to the task, did not impact the form-related performance either (Figure 7D).

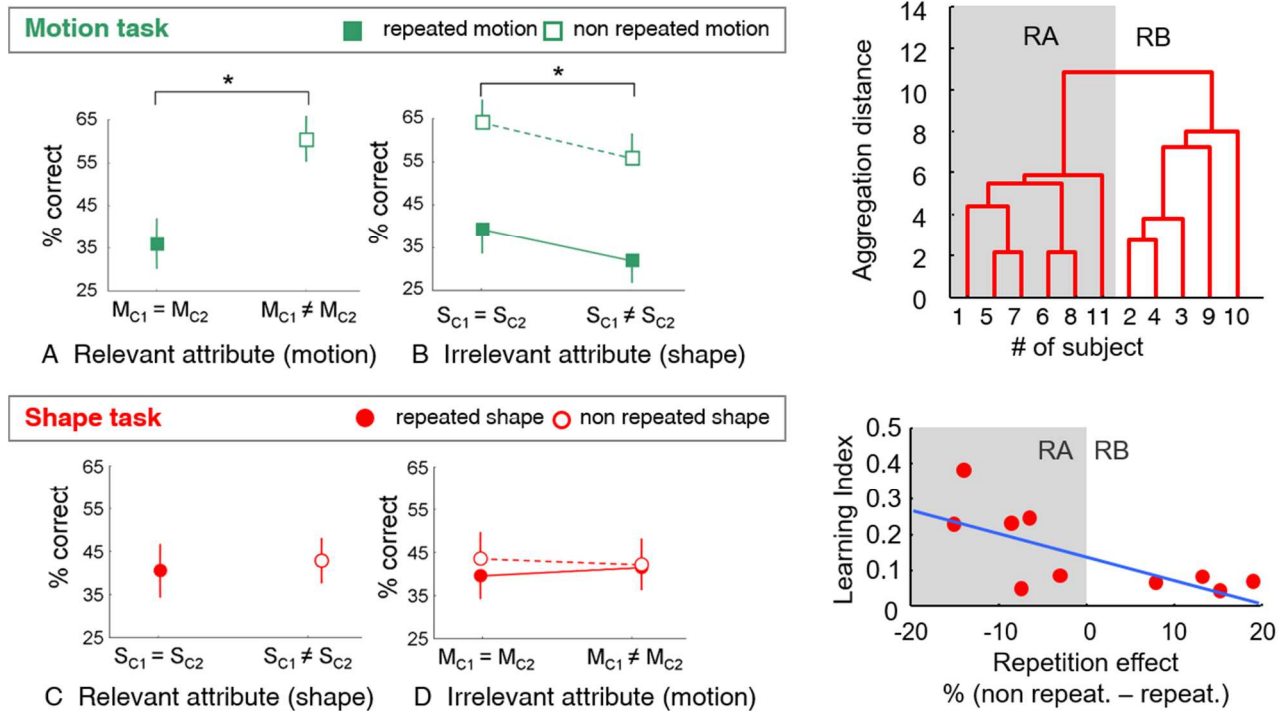


Figure 7. Results of the RSVP protocol. (Left) Performances in the motion and form tasks, depending on whether the attributes are repeated ($M/S_{c1} = M/S_{c2}$) or not ($M/S_{c1} \neq M/S_{c2}$). (Upper right) Subjects can be segregated into two statistically different groups showing either repetition blindness (RB) or repetition advantage (RA) in the form task. (Lower right) The repetition effect appears correlated to the learning index, which is inversely related to the initial ability of the subject of perceiving 3D shape from motion at the beginning of the training. Adapted from Miskiewicz et al., 2008.

Because repetition blindness is classically found when repeating static shapes, the absence of repetition blindness for the form task was rather surprising. Why should structure-from-motion stimuli suppress this effect? A closer look at the results of the form task showed that the participants could in fact be segregated into two statistically distinct groups (Figure 7 upper right). Five participants then revealed a clear repetition blindness effect, while the six other appeared to experience repetition advantage (RA). This behavioral difference was found related to the performance of the participants in the training phase. Precisely, the repetition effect was correlated with the evolution of participants' performances in the shape task during the training phase (learning index, Figure 7 lower right). As the training phase aimed to bring all participants at a similar level of performance (80% correct identification), the greater the learning index, the poorer the performance at the beginning of the experiment. In other words, repetition blindness was only observed in subjects who reached the required performance right from the beginning of the training. We specifically checked that the two groups showed no performance difference in the motion task, and as a reminder, both groups showed repetition blindness for motion direction. Consistently in this task, both groups were also able to reach the required performance of 80% correct from the beginning of the training phase.

Discussion

Overall, this study provided two new and paradoxical results:

1) Although we used *structure-from-motion* stimuli, the repetition of motion direction had no impact on shape perception, but shape repetition facilitated motion perception (Figure 8);

2) Repetition blindness appeared associated with a ‘spontaneous’ ability to identify the type of the stimulus (in practice, ability to reach 80% correct response with minimal training for the motion and/or the shape task), while the participants who necessitated more than four training sessions to reach 80% correct response in the shape task experienced repetition advantage.

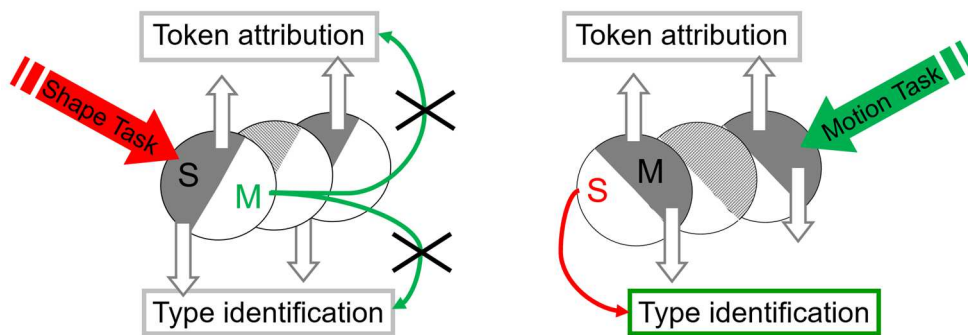


Figure 8. Interactions between motion and form observed in the shape and motion tasks. Motion repetition impacted neither identification nor token attribution in the shape task (left). Shape repetition facilitated motion direction identification (right). Adapted from Miskiewicz et al., 2008.

This repetition blindness vs. repetition advantage is reminiscent of the suppressive masking effects observed for suprathreshold stimuli on one hand (e.g. attention blindness) as opposed to the facilitatory priming effects observed for subliminal stimuli on the other hand. It is also consistent with a RSVP study showing repetition blindness for words but repetition advantage for non-words (Coltheart and Langdon, 2003). In this study, the authors proposed that repetition blindness is limited to items with pre-existing orthographic or lexical representations. Here this could correspond to all participants having a pre-existing representation of motion direction, while only a sub-group having a pre-existing representation of the 3D structure from motion. Yet, which mechanism should make a stimulus both easier to identify and store in memory, but harder to individuate?

Repetition blindness has been attributed to a *failure* of token attribution (Kanwisher, 1991) and especially a failure of the contextualization process, which is the assignment of the stimulus instance to a specific temporal and spatial context. Alternately, repetition blindness could also be considered as a *success* to merge interrupted visual inputs (between blinks or saccades for instance), and interpret them as one stable perception of the same object. This can explain why repetition blindness is reduced when a static object is repeated with two very different orientations (Harris and Dux, 2005). Such changes are barely compatible with the stability expected from a single object and may rather be interpreted as two different objects. Then, existing internal representations of the stimulus may help to maintain the ‘object file’ (Kahneman et al., 1992) open, and thus stabilize the perception in the absence of continuous or consistent inputs. This is also in line with more recent results showing that the level of semantic awareness associated with faces affected the recognition of those faces in an episodic memory task (La Corte et al., 2012).

Let us now come back to the observation that motion direction had no impact on form perception. This suggests that object identification was independent of motion direction. Such conclusion is consistent with our postulate that perceiving the 3D motion is *not* an intermediate stage of structure-from-motion (SFM) processing, but rather an end product of this processing just like 3D shape.

The reverse observation that form repetition influenced motion identification is more puzzling because it suggests that 3D motion processing could depend on shape perception. This direction of interaction is at odds with the observation that motion identification was usually faster than shape identification. However, the delayed response at the end of the trial also allowed interactions to occur after the initial extraction/perception/encoding of motion and form. Hence, the observed influence of (slow) shape on (fast) motion is likely related to a later process, e.g. recall or storing during the delay. In addition, our previous results suggested that form-related activity might be more robust and independent of the on-going task than 3D-motion-related activity. The observation that the encoded shape can influence the motion task but not the other way round is consistent with this assumption: motion information might not be 'maintained' enough to influence another percept when it is not the focus of the task.

In summary, although 2D motion processing is a prerequisite for 3D structure perception, we found the 3D structure has an influence on 3D motion perception, but we did not find any effect of motion direction on 3D structure identification. Moreover, motion and form features did not influence each other at the individuation level. The next study hence questioned the timing of motion and shape processing: can we determine a cascade of activity compatible with such behavioral observations?

Publication: Miskiewicz A, Buffat S, Lorenceau J, Paradis A-L (2010) Temporal dissection of stimulus-driven and task-driven processes during perceptual decision about 3D SFM stimuli. IFBME Proceedings Series http://dx.doi.org/10.1007/978-3-642-12197-5_76 (attached in Annexes)

In this study, we used magneto-encephalography (MEG) to highlight the cascade of processing at stake when performing a perceptual task on a structure-from-motion stimulus. In usual conditions, processing stages such as sensory processing, attentional selection and perceptual decision likely overlap in time. We hence designed an experimental protocol with specific time constraints in order to distinguish the brain signals related to different stages.

Protocol and results at sensors' level

The stimulation sequence consisted of a 3D-structure-from-motion target presented shortly and flanked by two preceding and following masking stimuli. The masking stimuli were aimed at delimiting the processing duration for the 3D target (see Figure 10A). Figure 10B shows the activity evoked by a stimulation sequence with a 3D target. Figure 10C illustrates the MEG signal evoked by a stimulation sequence in the absence of a 3D target: the activity related to the second mask (at +90ms after the mask onset) delimits the time windows during which the 3D target can be visually integrated.

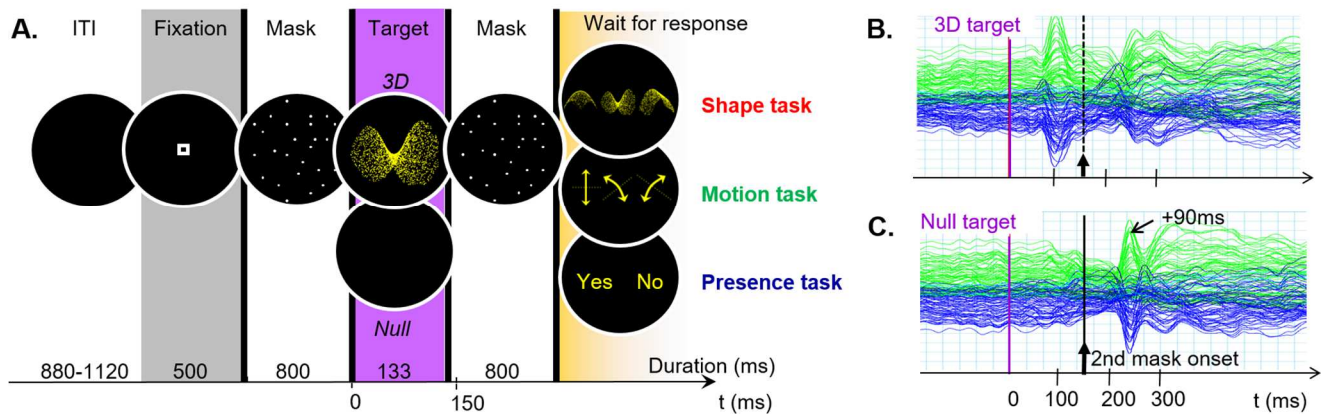


Figure 9. Activity related to a 3D-structure-from-motion stimulus in a time-constrained protocol. (A) Time course of the stimulation sequence. ITI: Inter-stimulus interval. (B) MEG signal evoked by a stimulation sequence including a 3D target. (C) MEG signal evoked by the stimulation sequence in the absence of 3D target. Adapted from Miskiewicz et al., 2010.

MEG activity has been recorded in the context of three different perceptual tasks. During the runs of Presence task, participants had to detect whether a 3D stimulus was presented or not in the stimulation sequence. For the Motion task and Shape task runs, instructions were to identify the motion direction or 3D shape of the presented target among three possible answers. The spatial organization of the response screen was randomized so that the participants could not choose their manual response in advance, in order to minimize the temporal overlap between perceptual and motor activity. That the response be delayed also gave similar conditions to that of the RSVP protocol. Yet, the observers knew which feature they had to attend before seeing the target so that we could assess the effect of the task on the target processing.

The analysis of the evoked magnetic fields first showed separate effects in time for stimulus and task, with significant stimulus effect (presence vs. absence) between 100 and 200ms around the occipital sensors, and significant task effect (Presence/Shape/Motion) between 300 and 320ms around the parietal and temporal sensors (Figure 10). Although later than the stimulus effect, this task-related effect still occurs during the presentation of the second mask, long before the response screen is displayed and a

motor preparation is possible. With the stimulus- and task-related effects non-overlapping in time, we do not have any evidence of a direct effect of the task on the early stimulus processing. However, the precedence of the stimulus effect –between 100 and 200ms– with respect to the task-related effect –between 300 and 320ms– is compatible with one feature of the stimulus being able to influence the later response to the task.

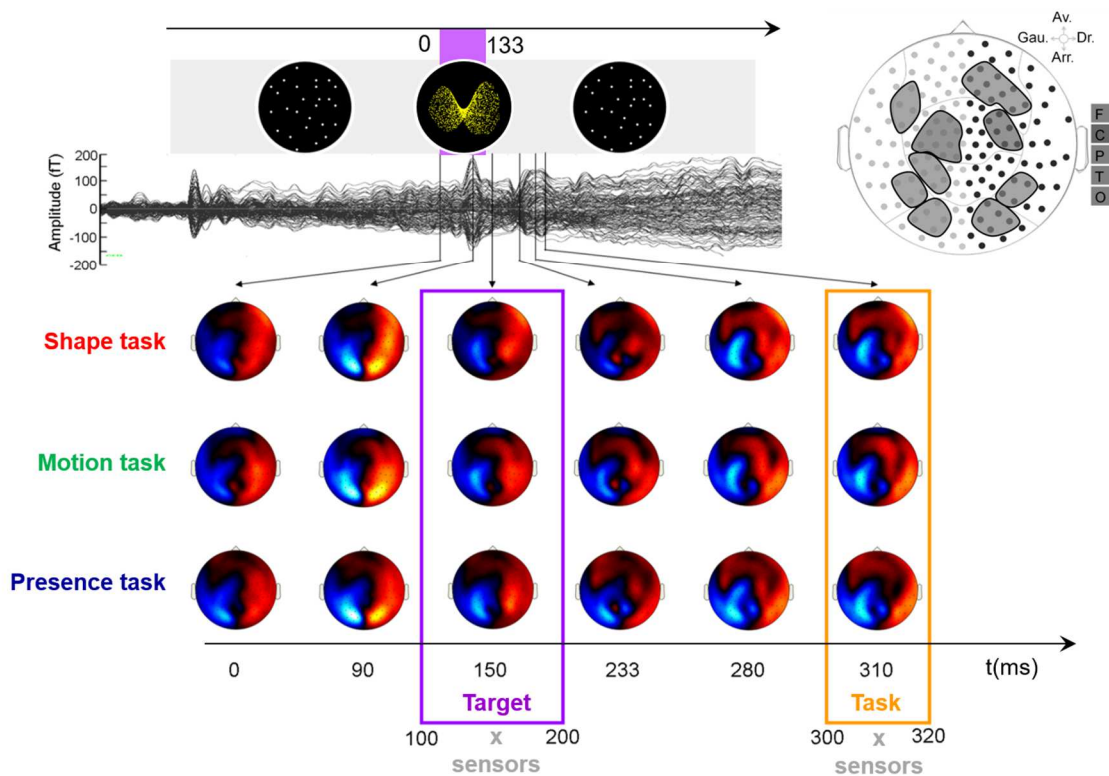


Figure 10. Time-separated effects of stimulus and task. The effect of the target (3D/Null) and the task (Shape/Motion/Presence) was tested along with groups of sensors (Top right). Significant target effect and target x sensors interaction were found between 100ms and 200ms, while significant task x sensor interaction was found between 300 and 320ms. The interaction with the sensors reveals that the target (resp. the task) does not only vary the amplitude but also modify the topography of activity, adapted from Miśkiewicz, 2009.

Time course of the sources of activity

After source reconstruction, the brain areas activated by the 3D target (Figure 11A) displayed notably different time courses, with peak of activity spread over a period from 90 to 270ms (Figure 11B). These time courses were globally consistent with the chronology described by Jiang *et al.*, 2008. Thus, we found similar early activity arising before 100ms in the occipital areas (V1) and a peak of activity in the medial part of the parietal cortex just before 300ms. We also found LOC activity temporally overlapping with parietal activity and sustained in time beyond 300ms, although the present LOC activity arose much earlier, as soon as 200ms (Figure 11, B vs. D).

The main differences were observed in late activity. Indeed, Jiang *et al.* (2008) described temporal activation between 350 and 400ms and re-activation of parietal and early visual cortex after 400ms, which were not observed in the present study. We assume this discrepancy is due to our masking stimuli, which seemingly suppressed differential activity between null target and 3D target beyond 350ms. Since the response mapping in Jiang *et al.* was not randomized, another possibility is that part of their late activity be related to the preparation of the motor response.

A second noticeable difference is the comparative timing of LOC and MT/V5: Jiang *et al.* (2008) reported a clear precedence of MT activity with respect to LO while here, both MT/V5 and LOC appeared activated simultaneously (see Figure 11B). This parallel timing could reflect that our MT and LOC signals

were partly confounded, perhaps because of a lack of spatial selectivity at the source level. However, this interpretation does not hold when we consider the time course of activity evoked by the stimulation sequence in absence of 3D target. In this case indeed, a peak of activity –consistent with the quick response of MT to motion onset– is observed in MT/V5 around 90 ms after the 2nd mask onset. In contrast, the corresponding peak is delayed around 270 ms in LOC (onset plus 140 ms), which does not support the interpretation that both sources were confounded. Instead, we suggest the specific time course of activity observed here in MT/V5 could be due to the presence of our dynamic masks. Because they maintain a continuous 2D motion input before and after the 3D target, they likely suppress the response evoked by the onset of 2D motion which occurs when presenting a 3D dynamic stimulus after a static baseline. This modification of activity in MT/V5 signal with the motion masks further supports the interpretation that MT/V5 is involved in processing 2D motion rather than coding 3D object features.

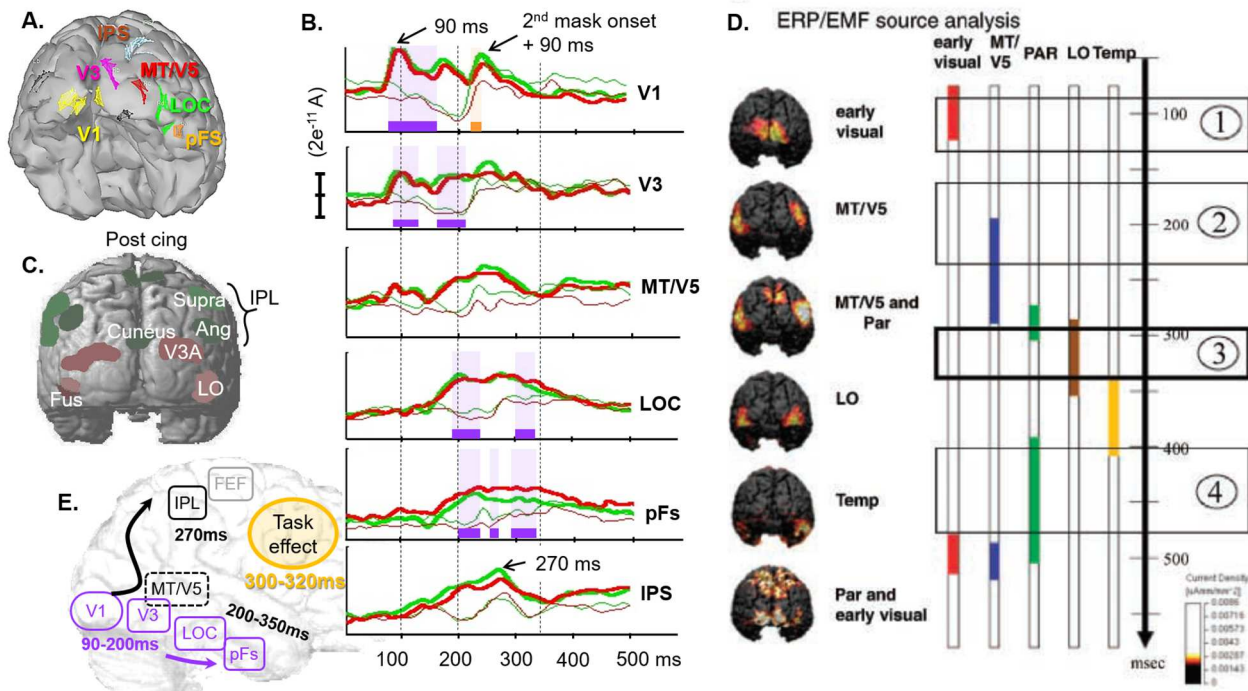


Figure 11. Time course of activity. Selected sources of MEG signal activated by the 3D target in the presence task (A), and their reconstructed time course of activity in the other two tasks (B). Bold lines correspond to the activity for the 3D target; Red and green code for the Shape and Motion tasks, respectively; periods of significant stimulus (resp. task) effect are highlighted in purple (resp. yellow). For comparison, regions of interest from the fMRI study (C), and the activation sequence described by Jiang et al. (2008) for the perception of 3D dynamic shapes in a protocol without time constraints (D). (E) Summary of the observed sources and their timing of activity.

Eventually, we observed a very particular pattern of activity in the intraparietal sulcus (IPs). The signal increased slowly with LOC activity and decreased rapidly after 270ms, long before the possible preparation of the motor response. The timing of the decrease for the 3D target is also coincident with the peak of activity visible in null target condition and likely evoked by the onset of the 2nd mask. A possible interpretation is that IPS activity increases until the information related to the 3D target is replaced/interrupted by information related to the 2nd mask. Interestingly, this pattern is consistent with cellular recording in monkeys suggesting that IPS accumulates information about moving visual stimuli as long as more information about the target is required and available (Huk and Shadlen, 2005). Given the complex relationship between cellular recording in monkeys on one hand and macroscopic MEG recording in humans on the other hand, additional data would be required to elucidate the questions put forward by this particular pattern of activity: does it actually reflect accumulating information? Does the IPS region process motion information only or does it integrate information from shape-processing areas as well?

Stimulus-driven vs. task-related activity

When directly assessing the source signal, the significant stimulus effect detected at sensor level appeared concomitant with the activity of the earliest visual areas (V1, V3). In contrast, the task effect was concomitant with stimulus-related activity of the later areas (LOC, pFS). However, we did not find any significant effect of the task in those areas (Figure 11B). Overall, none of the regions of interest involved in processing the structure-from-motion stimulus (Figure 11A) appeared consistently modulated by the type of feature targeted by the task. This negative result is in line with our previous fMRI results showing that the attentional selection of 3D motion and shape involved different areas from stimulus-driven activity. Here, the task effect observed at the sensor level rather seemed to arise from more anterior visual brain regions as well as right fronto-polar areas. We interpreted this frontal involvement as a possible effect of task difficulty (Mangina et al., 2009) and/or prospective memory required by the delayed response (Burgess et al., 2003). The following unpublished data may bring another insight about the possible involvement of anterior temporal areas as well.

Posters: Benmussa F, Dornbierer J-G, Buffat S, Paradis A-L & Lorenceau J (2012). Looking for the LOC with MEG using frequency-tagged natural objects. JoV August 2012, Vol.12, 511 (VSS) <http://dx.doi.org/10.1167/12.9.511>; <https://f1000research.com/posters/2249>. PhD work of F. Benmussa, co-supervised with J. Lorenceau, in collaboration with S. Buffat (IRBA). The project was supported by a doctoral contract from DGA to FB and REI grant n°2006 34 059 to JL.

The main objective of this study was to set up an MEG ‘localizer’ protocol aimed at delineating the brain areas involved in object recognition. We thus used clouds of points obtained from 3D scans of familiar objects (Buffat et al., 2014) as well as their scrambled versions (see Figure 12). To optimize the detection of MEG activity related to object perception, we further decided to “tag” the signal related to the stimuli with a specific frequency. Frequency tagging is associated with powerful signal at a known frequency, which allows to precisely identify the signal of interest. In that context, we can also analyze the magnetic signal “evoked” by the stimulus by considering each stimulation period as an event.

Protocol and results

Several visual features can be used to tag a stimulus. In this study, we compared three types of tagging related either to luminance or object identity (Figure 12).

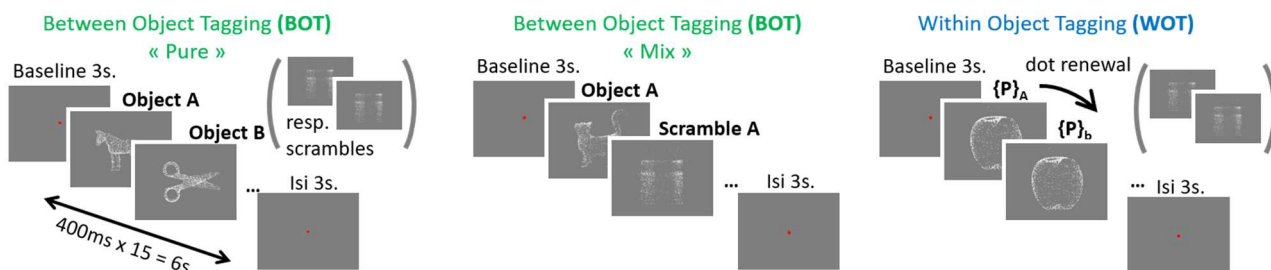


Figure 12. Frequency tagging protocol used to spot the activity related to object perception with MEG.

The first tagging condition, here called “Pure Between Object Tagging”, consisted in switching object shapes (resp. scrambles) every 400ms (i.e. 2.5Hz) or 83ms (12Hz). The second condition (“Mix”) alternated objects with scrambles. The third condition consisted in replacing dots of the cloud, thus inducing luminance tagging without changing the shape of the stimulus (“Within Object Tagging”). Preliminary analyses revealed that this within object tagging was poor at activating brain areas involved in object recognition. Also, 12Hz tagging conditions only induced low power activity. This later observation was consistent with a masking effect of each new object (resp. scramble) on the previous one, likely interrupting the later component of object processing, as suggested by the results of the above study.

We thus focused our analysis on the data recorded in the between-object-tagging conditions at 2.5Hz. We then computed the signal evoked by the stimulus transitions –i.e. the onset of a new object or a new scramble– on a time window of 400ms, and compared the four possible types of transitions (Figure 13A) in a two-factor ANOVA. A main effect of the stimulus appearing after transition (Object/Scramble) aroused around 170-185ms (Figure 13B, green). The associated sources of activity were located in the left lateral occipital cortex (LOC) at 170ms and bilaterally in the anterior temporal pole at 185ms. The mix/pure condition did not induce any significant effect *per se*. However there was an interaction between the appearing stimulus and the mix/pure condition, which can also be interpreted as a main effect of the stimulus preceding the transition (Object or Scramble). Although later and more spread in time than the activity evoked by the appearing stimulus, this activity related to the disappearing stimulus was found at the same location and reproduced the same temporal order: peak of activity at 190ms in the LOC, followed by anterior temporal activity around 230ms.

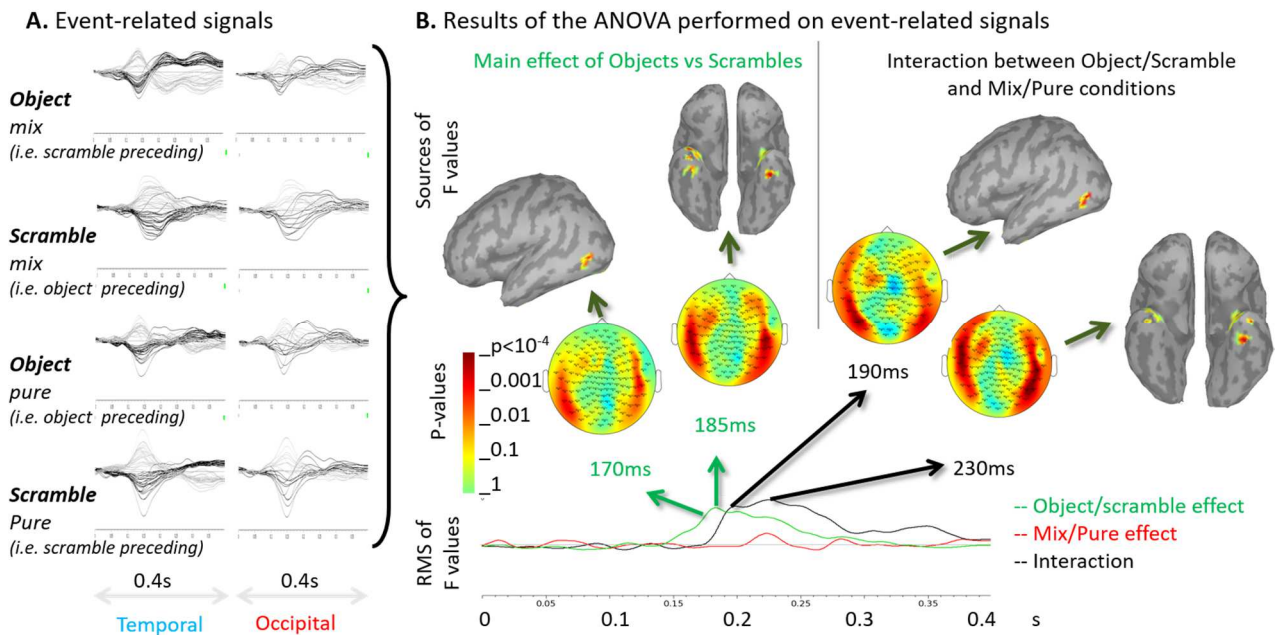


Figure 13. Two-way ANOVA. (A) Averaged MEG signal triggered by stimulus transition from scramble to object (Object mix); from object to scramble (Scramble mix); between objects (Object pure); between scrambles (scramble pure). (B) Effects of stimulation conditions on the evoked MEG signal.

The parametrical tests carried out on all sensors and time samples were supplemented by a non-parametric “clustering” analysis (Maris and Oostenveld, 2007), which allowed to assess the statistical significance of the observed effects while overcoming the issue of multiple comparisons raised by the point-by-point analysis. In practice, all signal samples with uncorrected $p < 0.05$ were clustered based on time and space adjacency (ie. consecutive time samples and sensors less than 4cm away). Each cluster was then assigned the sum of T-values of all its constitutive samples. The same clustering procedure was then repeated a thousand times with the condition labels randomly reassigned to the original dataset, in order to model the null hypothesis. For each randomization we selected the maximal “sum of T” and used it to build an estimated distribution of this statistical value under the null hypothesis. Because this method uses the maximum statistics, it intrinsically controls for multiple comparisons. We then compared the value of each original cluster with this distribution: clusters with values greater than 99% of the distribution were considered significantly activated with a probability of false positive smaller than 0.01.

This approach confirmed there were two significant clusters associated with the Object minus Scramble contrast: one including left occipito-temporal sensors and lasting from 159ms to 273ms; and its symmetrical counterpart including right occipito-temporal sensors and lasting from 152ms to 286ms (Figure 14A). The mid-temporal sensors, which likely reveal LOC activity, are those involved in the Object minus Scramble effect for the longest duration. However, we also observed a sustained effect in the anterior temporal sensors, which corresponded to a powerful activity located in the anterior temporal lobe and Orbito-Frontal areas after source reconstruction, and maximal between 180ms and 220ms (see Figure 14B and C).

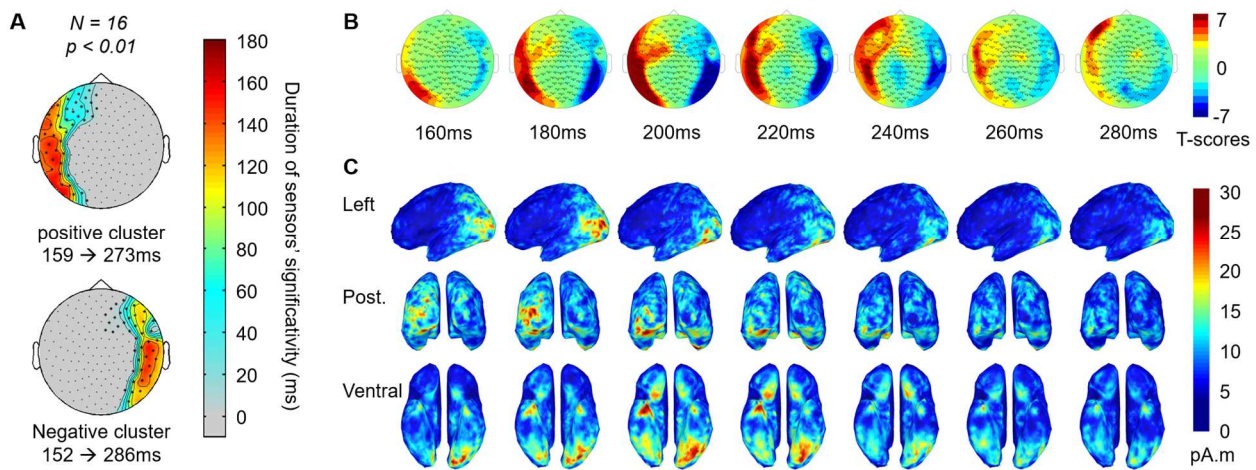


Figure 14. Object minus Scramble effect. Significant clusters of activity ($p < 0.01$, $N = 16$) determining the time window of the effect between 150 and 290ms. (B) Evolution of the activity topography across the time window of interest, and corresponding source reconstructions (C).

Anterior Temporal Pole

We hardly found fMRI reports of anterior temporal pole activity in the context of visual object recognition. This is not so surprising since strong magnetic susceptibility artifacts tend to dramatically lower the signal recorded with fMRI in this region, and studies designed for visual object recognition are likely to focus on occipital and posterior temporal areas rather than tune the acquisition sequence to record the anterior temporal pole. The anterior temporal poles were rather found associated with semantic memory (Martin and Chao, 2001) as well as social and emotional processing (Olson et al., 2007). Previous neuropsychological and PET data (Damasio et al., 1996) however suggest that these regions could be involved in processing lexical information. Some TMS studies (Lambon Ralph et al., 2009; Pobric et al., 2007) and a meta-analysis (Visser et al., 2010) suggest that the anterior temporal pole is implicated in semantic tasks across various input – words, pictures, objects, sounds, smells – and output – written and spoken – modalities. They further propose that this region processes and stores amodal semantic representations associated to sensory stimuli, and acts as a ‘hub’ allowing conceptual manipulation and information exchange between different modalities. Globally, its involvement in the present study would be consistent with the fact that our stimuli were familiar objects belonging to different semantic categories (namely fruits, vehicles and tools), and that participants were instructed to report a maximum number of seen objects after recording, thus requiring lexical storage.

Study comparison

With 400ms duration for each stimulus, this study imposed much less time constraint on object processing than the previous study. It is then likely that the evoked magnetic wave could fully develop before the activity was disrupted by the onset of a new stimulus onset. The time issue however is unlikely to account for the absence of activity in the anterior temporal lobe with 3D structure from motion stimuli. Indeed, the significant cluster of activity including the ATL was spread over a 160-280ms interval, which perfectly overlaps with the time interval of significant activity in the 3D structure from motion study (see Figure 15A and B). Then, it is more likely that the difference comes from the nature of the stimuli, especially the use of familiar and nameable objects vs. 3D geometrical surfaces.

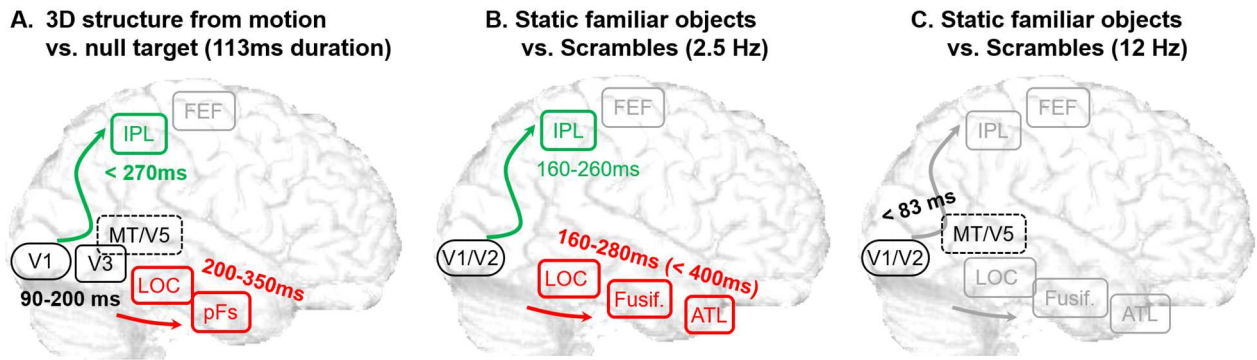


Figure 15. Comparative summary of the previous MEG results. Localization and timing of the stimulus effect when comparing (A) the presentation of 3D structure from motion with respect to a null target (Miskiewicz et al., 2010) or (B and C) Static familiar objects with respect to their scrambled counterparts at 2.5 Hz and 12Hz respectively (Benmussa, 2013).

It is noteworthy, that activity related to the 3D structure-from-motion stimuli could still be observed at the source level beyond the timing of the response to the second mask in the null target condition (see Figure 11B in LOC and pFs). In contrast with this, the tagging protocol did not allow us to identify activity beyond the onset of the next stimulus i.e. after 400ms at 2.5Hz and 83ms at 12 Hz. There was however a risk of temporal aliasing, meaning that late components of the response could be folded in the observation period and thus misinterpreted as early components. The risk was especially high for the 12Hz presentation frequency since the observation window was limited to 83ms. However, the activity evoked by the tagging conditions at 12Hz, which did not develop beyond occipital regions and was much weaker than the activity at 2.5Hz, rather suggests that late components were actually suppressed. This interpretation is also consistent with a subsequent behavioral study in which participants had to identify a target among a rapid visual serial presentation at different presentation frequencies: participants were not only worse at identifying a target object when the presentation frequency was higher, they also revealed much less confident in their responses, which suggested an absence of conscious perception.

INTEGRATION AND SELECTION

With separate timings of activity for stimulus and task, the previous results were in favor of independent task- and stimulus-related activity. However, we also found that repeating the form feature had an effect on the motion perception task, which supports that processing a non-attended feature of a stimulus can interfere with the task performed on another feature of the same stimulus. Then, I wished to further investigate the links between feature perception, attentional selection and task, and their neural correlates.

Our RSVP results further suggested that form repetition proceeded like a priming effect on the perception of motion. However, contrarily to the usual priming conditions, the primed feature (i.e. shape) was not the one targeted by the task (i.e. motion), so the following questions arose: Could an attentional priming directed at one feature enhance the perception of another feature of the same object? This question was in line with the more general theory proposing that conscious visual perception depends on attention. Indeed, we could imagine that repeating the form may enhance the attention paid to the overall stimulus, and thus facilitates the conscious perception of its motion in the motion task.

Publication: Liu Y, Paradis A-L, Yahia Cherif L & Tallon-Baudry C. (2012) Activity in the lateral occipital cortex between 200 and 300 ms distinguishes between physically identical seen and unseen stimuli. Front Hum Neurosci 6: 211. <http://dx.doi.org/20.3389/fnhum.2012.00211>

Although the role of attention in conscious perception had been questioned (Koch and Tsuchiya, 2007) and even challenged by evidence that the neural bases for conscious perception and spatial attention are dissociated (Wyart and Tallon-Baudry, 2008), the status of feature-based attention remained to be explored. Here, we investigated the possible relationships between feature-based priming and conscious perception using color and static orientation. These two features do not depend on motion processing and are not likely to interfere because of a common early extraction process. If an interaction was found between those features, it would rather be due to attentional mechanisms operating at the object level.

Protocol and results

This work has been performed by Ying Liu during her PhD, co-supervised with C. Tallon-Baudry. In this study, we recorded MEG activity while testing the effect of color priming on static orientation perception. To this end, we used a protocol previously designed to assess interactions between spatial attention and perceptual consciousness (Wyart and Tallon-Baudry, 2008). The previous spatial priming was replaced with color priming (Figure 16).

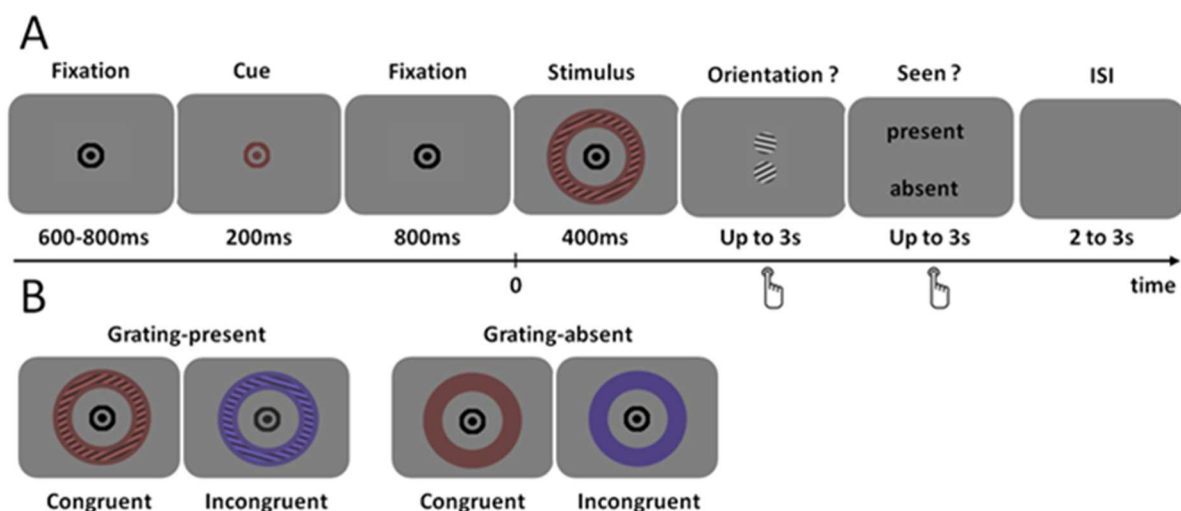


Figure 16. Protocol to assess possible interaction between color priming and orientation perception during MEG recording. (A) Time course of a typical trial, and (B) the four types of 'Stimulus' used in the protocol. The grating-present stimulus were used in 87% of the trials, and the color of the Stimulus was identical to that of the Cue (i.e. Congruent) in 65 % of the trials. We thus manipulated color congruency between the target stimulus and a prior visual cue irrelevant to the task. Two questions were asked at the end of the trial; by gathering both objective and subjective answers, we could determine whether the observers consciously perceived the grating in the colored ring. Figure from Liu et al., 2012.

One objective of this study was to determine whether the neural correlates of consciousness could depend on feature-based attentional selection, with the assumption that the color cue presentation would induce enhanced attention to a target object with the same color. Since the behavioral results did not reveal any effect of color congruency on orientation perception, we could not validate that color repetition (congruency) induced enhanced attention to the target stimulus. We then analyzed the MEG activity related to conscious perception, color congruency and their possible interactions.

By comparing seen and unseen present stimuli, we found correlates of conscious perception between 200 and 300ms. We could further localize the main sources of this activity bilaterally in the lateral occipital complex (rLO et ILO, Figure 17A). Just as color congruency did not affect the behavioral response to the grating, it did not affect the LO activity related to conscious perception either, further suggesting that the co-localized color and orientation features did not influence each other and were processed independently.

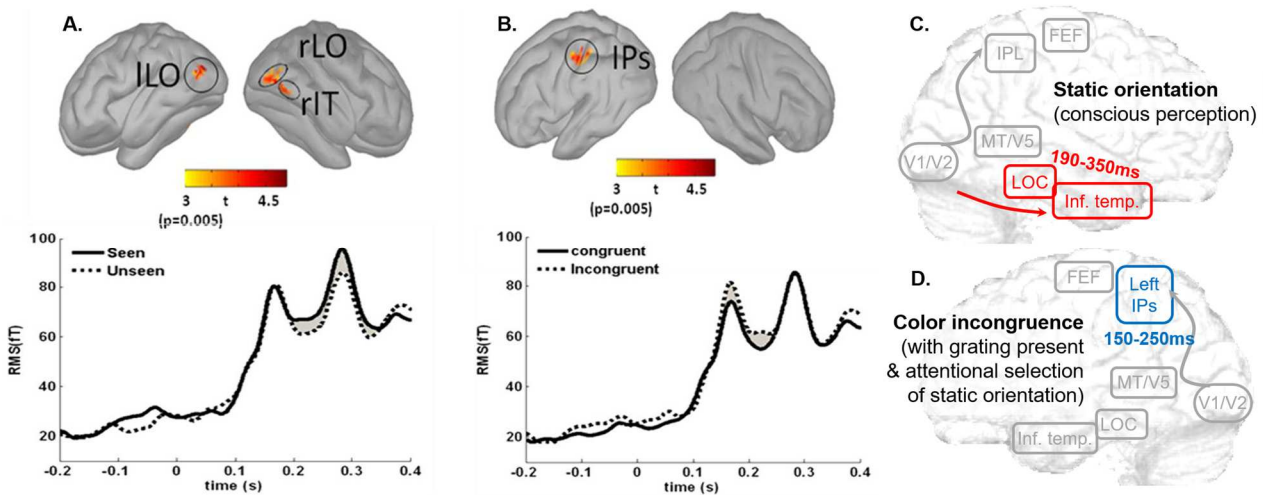


Figure 17. Localization and timing of MEG activity evoked by consciously seen stimuli (A,C) and color congruency (B,D). Significant seen-unseen difference in bilateral lateral occipital areas and right inferior-temporal cortex, from 190 to 350ms after stimulus onset; significant incongruent-congruent difference in left IPS from 150 to 250ms, for grating-present stimuli only; adapted from Liu et al., 2012.

Compared to congruent colors, incongruent colors evoked more electrophysiological activity in IPS at 150-250ms. As stated above, this color (in)congruence effect did not depend on whether the presented grating was consciously perceived or not. However, it depended on whether the grating was physically present or not.

Intra-parietal sulcus

In the literature, left IPS activity has been related to the selection of low saliency stimuli (Mevorach et al., 2009), in particular when more salient distractors are present. Here, the incongruent color could represent a distractor and the grating the low saliency stimulus to select.

Thus the present IPS activity could be specifically related to the processing of a feature irrelevant to the task. This does not support the existence of an active contamination of one feature by another through a possible attention effect at the level of the object, nor an active binding of the features belonging to the same object. Instead, the present results are rather in favor of an active selection mechanism occurring between competing co-localized and/or co-occurring features to allow the independent processing of each feature.

Feature selection

Since color repetition did not prove to enhance attention to the stimulus target, we cannot conclude that the effect of shape repetition observed in the RSVP protocol was due to an attentional enhancement of all perceptive features associated with the repeated object.

On the contrary, the present results suggest that an active processing is required to be able to selectively analyze the feature relevant to the task among two co-localize features. This seemed to occur especially when the irrelevant feature was incongruent and may have acted as a distractor with respect to the main task. With this perspective, a shape transition occurring during the motion task of the RSVP

protocol is likely to induce extra-processing load in order to select the motion feature relevant to the task. The advantage related to shape repetition could then be interpreted as an absence of detrimental effect related to shape transition.

This feature-selection interpretation further questions the asymmetry observed between motion and shape. Mevorach and colleagues suggested that two different selection processes occur depending on whether the relevant stimulus is more or less salient than the distractor (Mevorach et al., 2009). In the case of shape and motion, does it mean that one feature is more salient than the other? The relatively low activity related to 3D motion in passive viewing might be interpreted as the motion feature being less salient. Nevertheless, the fMRI results obtained in active conditions did not reveal any consistent left/right parietal asymmetry for motion vs. form that could support this view.

Publication: Caclin A, Paradis A-L, Lamirel C, Thirion B, Artiges E, Poline J-B, Lorenceau J (2012). Perceptual alternations between unbound moving contours and a bound shape motion engage a ventral/dorsal interplay. Journal of Vision. <http://dx.doi.org/10.1167/12.7.11>

We have seen that motion and shape information were processed by distinct cerebral areas. However, both features have to be combined to produce the unified and coherent percept of a moving object. We have also seen that the areas involved in perceiving the 3D motion of an object are different from the areas usually associated with (2D) motion processing. It is thus important to dissociate the neural activity related to the conscious end percept from that related to the physical specificities of the stimulus, and better understand how the visual system translates the analysis of a visual input into the representation of a perceptive attribute. The objective of the fMRI study presented here was thus to identify the brain areas sustaining the binding of distinct visual elements into the unified percept of one moving shape.

Protocol and results

In this study, stimuli were line segments arranged into a diamond shape (Figure 18), with each segment following a vertical oscillatory movement. This stimulus is called “bistable” because it is compatible with two visual interpretations: the observer can either perceive several unbound elements moving back and forth, or a rigid diamond following a circular trajectory (Figure 18A). The observer can spontaneously jump from one perceptive interpretation to the other. However, some physical characteristics of the stimulus can favor one interpretation or the other. For instance, segments with low-contrast ends (Figure 18B) contribute to spatial integration and promote the perception of a diamond. In contrast, segments made of dots are more easily perceived as independent elements. Yet, if the dots constituting the segments are moving along the segment orientation thus blurring the information about their relative positions, the bound interpretation returns to the fore (Figure 18C). Finally, compared to the arrangement into a closed shape like the diamond, an arrangement in chevron promotes the unbound interpretation (Figure 18D). Since it is possible to progressively modify those contrast, motion or configuration characteristics in time, it was also possible to drive changes of perceptual interpretation (Figure 18E).

We analyzed the fMRI activity related to the bound and unbound percepts, when perception changes were either spontaneous or evoked by physical changes of the stimuli. Comparing bound and unbound perception into previously defined regions of interest revealed enhanced activity for the bound percept in the ventral areas and greater activity for the unbound percept in hMT.

Supplementary analyses revealed that ventral and dorsal areas were similarly activated whether the stimuli were physically modulated in time or not, so that the activity of those regions appears to mainly depend on the subjective perception. This observation supports the idea that the brain areas sustaining subjective perception are not necessarily processing the physical characteristics of the stimulus. This further suggests that the perception-related areas described here could be part of a generic network involved in spatially binding sparse visual elements into a unique moving shape.

With this perspective, the mirroring responses observed between the ventral fusiform area and the dorsal hMT area could reflect a dynamic weighting of the evidence in favor of one interpretation or the other (e.g. more activity in MT in favor of several moving elements, more activity in the fusiform in favor of a coherent shape).

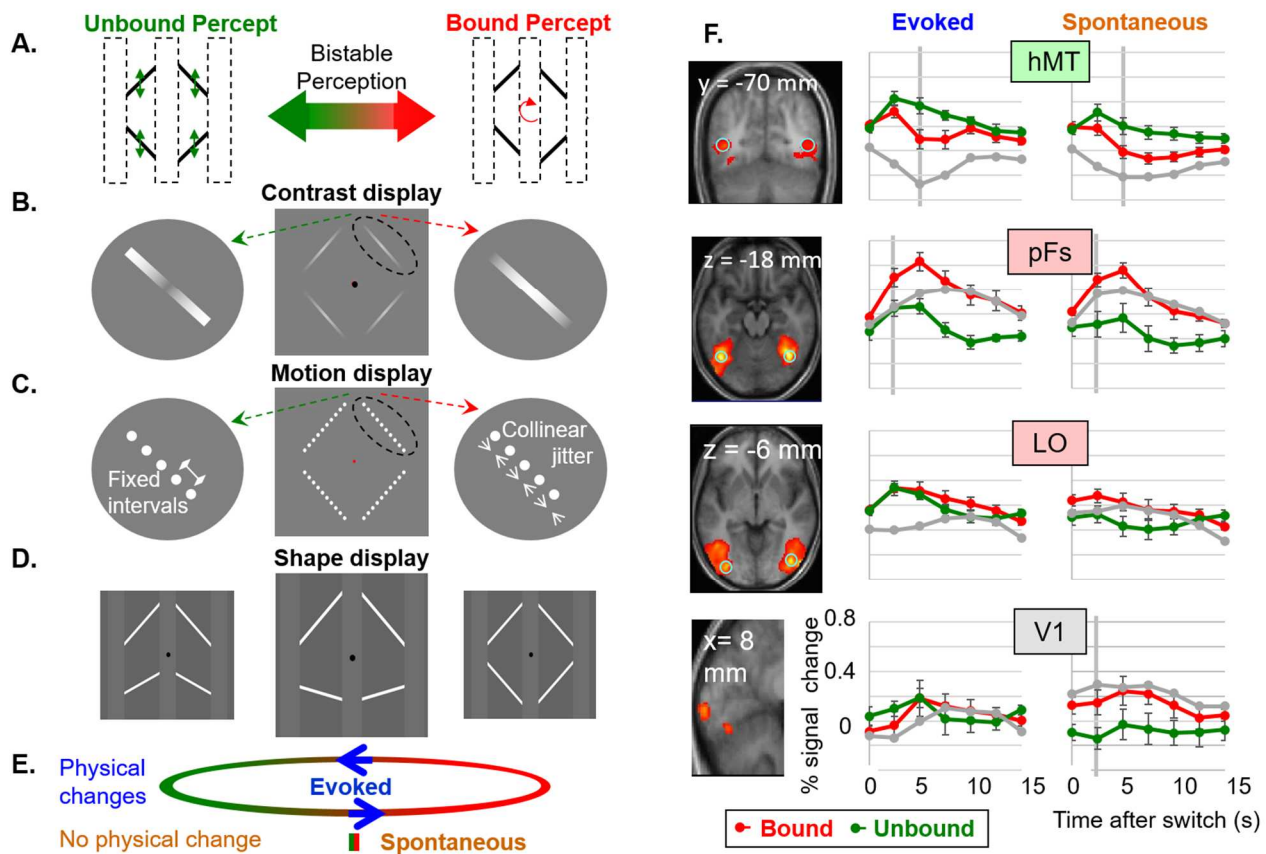


Figure 18. Neural bases of perceptual binding. (A) Bistable perception switching between bound and unbound percepts. (B,C,D) Three types of stimulus modulation used to induce perception switches –segment contrast, local motion and shape arrangement. (E) There were two types of perceptual switches –those evoked by the physical variations of the stimulus and spontaneous switches occurring without stimulus changes for an intermediate value of the visual parameters. (F) Activity evoked by the transitions toward bound perception in red (resp. unbound in green) in previously determined regions of interest. The gray line displays the difference between the two responses, and the gray bar indicates the first time of significant difference between the responses to the two percepts, adapted from Caclin et al., 2012.

Discussion

The pattern of activity described here is somehow reminiscent of the competing activity observed between the dorsal and ventral pathways when comparing the activity related to 3D motion and form (Figure 3, p12), but with notable differences however. Here, the dorsal activity did not extend beyond hMT/V5. By contrast with the 3D features, which both required to analyze the 2D motion distribution at the level of hMT and were perceptually segregated through a competition engaging downstream areas of the dorsal pathway, the present bistable stimulus seemed to engage the early stage of 2D motion analysis in the competition.

In addition, a closer look at the time course of activity revealed that the balance of activity between pFs and hMT was not symmetrical. Although, the activity evoked by perceptual transitions was always positive in the fusiform region, it was either positive –toward the unbound percept– or negative –toward the bound percept– in the hMT+ region (see Figure 18F). This asymmetry may reveal a predominant role of shape processing in the binding mechanisms observed here. In line with this hypothesis we found that the ventral activity -related to shape- preceded the medio-temporal activity –in the motion area: strong activity of pFs may down modulate hMT activity, while weaker shape-related activity would prevent this down modulation (Figure 19).

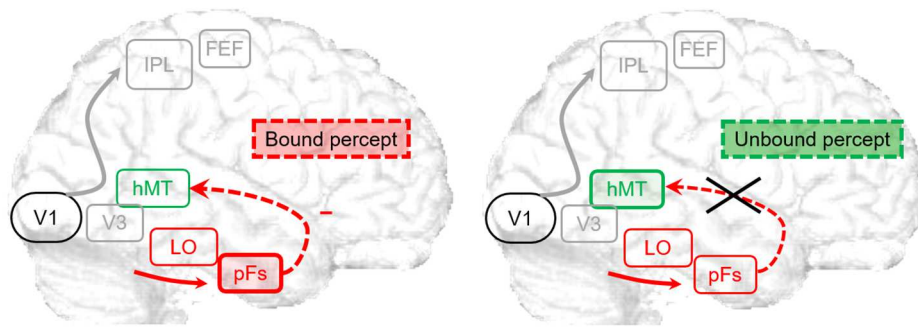


Figure 19. Proposed mechanism for perceptual binding. Transitions to a bound percept were associated with strongly enhanced activity in pFs possibly preceding decreased activity in hMT. Transitions toward an unbound percept were associated with a transient and slight enhancement of activity in pFs, along with a rather strong response of hMT. The asymmetrical balance of activity between hMT and pFs is compatible with pFs activity driving both the percept and the activity decrease in hMT.

As the time course of activity in fMRI was not reliable enough to definitively conclude on the relative timing of the two regions, we cannot exclude that enhanced activity in hMT could also down-modulate pFs activity in return, without totally suppressing its activity. Overall, it is noteworthy that a similar predominance of ventral activity with respect to dorsal activity was found in two different fMRI studies, and that this predominance is consistent with the behavioral results of the RSVP protocol, showing that shape information could influence motion perception –but not the other way round.

Publication: Paradis AL, Morel S, Seriès P & Lorenceau J (2012). Speeding up the brain: when spatial facilitation translates into latency shortening. *Front Hum Neurosci* 6: 330. <http://dx.doi.org/10.3389/fnhum.2012.00330>

To bring an end to the question of motion and shape interactions, I will quickly present a last study showing how our motion perception can reveal some brain tricks to optimize the extraction of shape information.

Working hypotheses and protocol

After a model published in 2002 (Seriès et al., 2002), when a Gabor patch is presented to an orientation-selective cell in V1 (cell 1, Figure 20A) this cell propagates subthreshold facilitatory activity to its neighboring cells selective for a similar orientation (e.g. cell 2). If a second Gabor patch, with similar orientation, is presented to such a cell at a time compatible with the neural propagation of the facilitation signal (t2), its response should be advanced. If the preferred orientation or relative positions of the visual fields are not compatible (e.g. cell 3 whose preferred direction is not aligned with that of cell 1), no facilitation should be observed. The aim of this study was to highlight neural correlates of this model in the visual cortex.

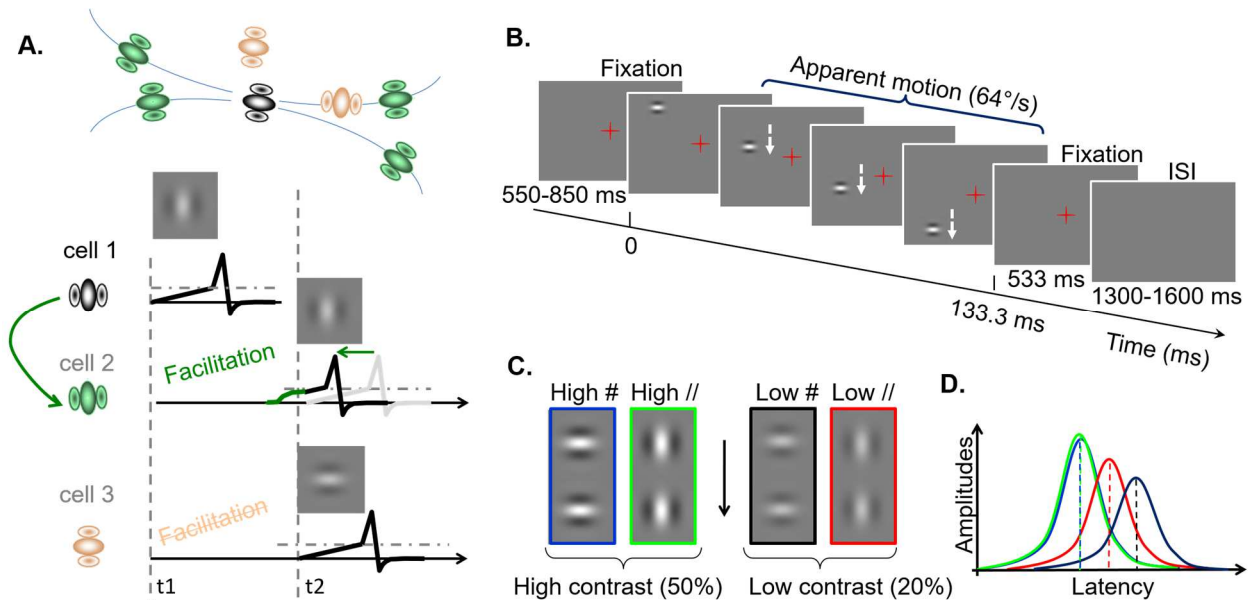


Figure 20. Working hypotheses and protocol. (A) Principle of lateral facilitation: an activated cell (in black) may propagate a facilitation signal to cells with aligned receptive field and similar orientation preference (in green; examples of cells with non-compatible receptive fields or orientation preference in orange). (B) Time course of a trial. (C) Experimental conditions. (D) Expected effect on the MEG signal.

MEG activity was recorded while Gabor patches were presented in sequence along a vertical path (Figure 20A). The timing and successive positions of the patches were chosen so that facilitation effects could apply (Figure 20B). Such sequence of stimulation resulted in rapid apparent motion. Because facilitation effects theoretically depend on the orientation of the stimuli and the contrast of the stimuli, four types of stimuli were used (Figure 20C). The model of activity in V1 predicts that high contrast stimuli should evoke high-amplitude and short-latency responses, hardly sensitive to facilitation (Figure 20D, expected similar green and blue signals). In contrast, low-contrast stimuli being much weaker, they require longer integration to trigger a neural response and are thus more susceptible to benefit from the orientation-related facilitation. In this case, we expected to observe different responses depending on whether the stimuli were aligned or not (Figure 20D, larger and earlier response expected for aligned stimuli, in red, compared to non-aligned stimuli, in black).

Results and interpretation

Amplitude and latency were measured on the averaged signal of the sensors with maximal response to the sequence of non-aligned high-contrast stimuli (Figure 21A). The effect of the conditions were visible on individual signals which exactly followed the predictions (compare Figure 20D and Figure 21B). At the group level, we could find a significant effect of the Gabor orientation on the latency for low-contrast stimuli only (Figure 21C). Although a similar trend was found with the response amplitude, the effects were not significant.

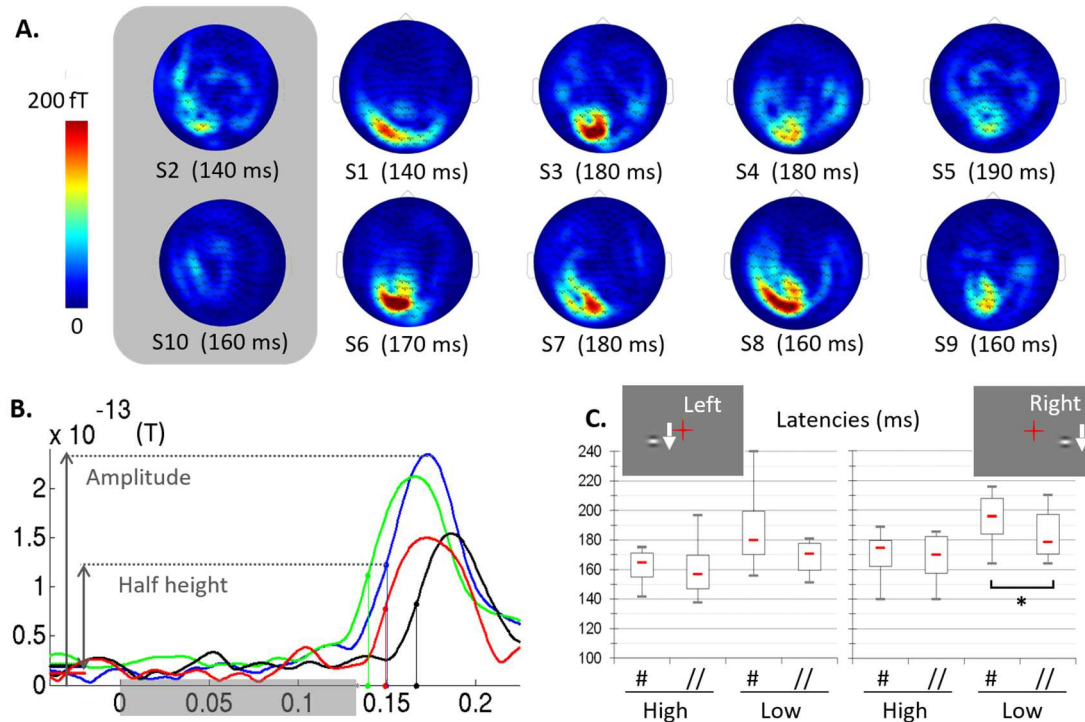


Figure 21. Results. (A) Sensors with maximal activity for the non-aligned high-contrast stimuli; two datasets were excluded for non-significant activity in this condition (grey insert). (B) Example of individual signals illustrating the expected effects. The gray bar indicates the period of presentation of the Gabor patches. Amplitude and latency were measured at the response peak. (C) Significant effect of orientation on response latency for low-contrast patches on the right. Adapted from Paradis et al., 2012.

Although this study used apparent motion stimuli, the results should be interpreted with respect to shape perception. Indeed, the rapid presentation of aligned Gabor patches is not a stimulation the visual system has to deal with very often. It is much more frequent to face objects which have interrupted or attenuated contours because of inconstant illumination or complex multicolor background. In this case, the model presented here suggests that high-contrast portions of contour may serve as seeds which propagate facilitatory signal to the neighboring oriented cells susceptible to detect less contrasted portions of the same contour. With such advantage, the visual cells are not only more likely to detect the fading contour but their response is also speeded up thus making up for the firing delay due to low contrasts. Overall, this mechanism could contribute to synchronize the firing of cells 'seeing' the same contour, and thus facilitate the transmission of their signals to later processing stages.

Up to now, I have been presenting perceptual processes occurring in static observers, and most often in visual fixation conditions. This new part dramatically changes perspective since I will now consider observers who are actively moving, namely ‘navigators’, and a larger-scale space. With the change in dynamics, a new dimension arises and visual 2D motion inputs do not only give rise to information about the form and motion of external objects but also convey information about self-motion.

If we try to schematize a navigation situation, rather than the hierarchical processing usually favored in the framework of perception, we should now consider a loop (Figure 22). Indeed, if the sensory processing performed during navigation still informs the decisions made by the observer, the actions executed downstream in turn directly impact the sensory processing itself by inducing an expectable variation of the sensory inputs due to self-movement.

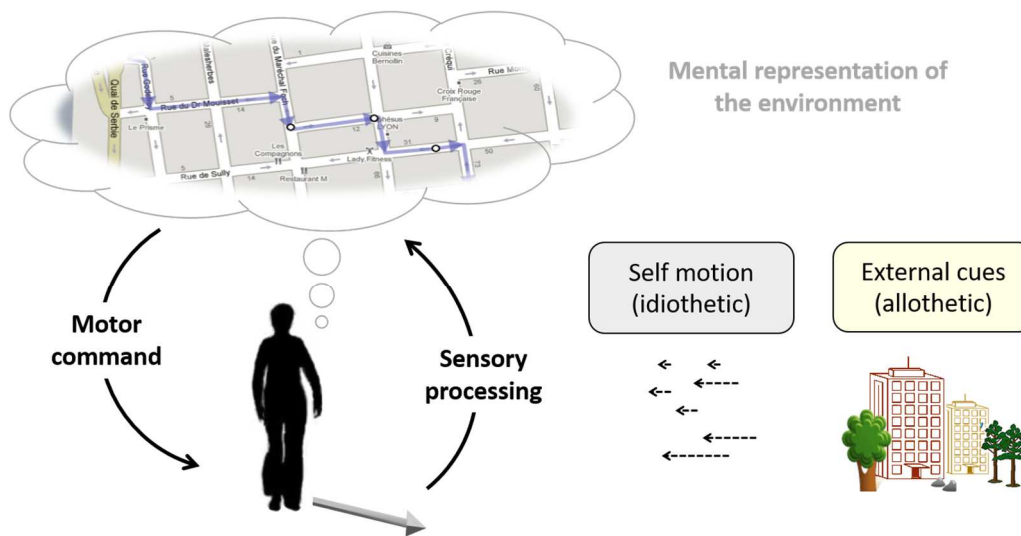


Figure 22. The navigation loop. During exploration or goal-directed navigation, sensory processing allows us to gather information about our self-motion (idiothetic information) on one hand and about the environment (allothetic information) on the other hand. Both types of information are used during navigation to feed our internal representation of the environment and update our position and orientation with respect to this representation. In turn, we use this internal representation to develop complex navigation strategies which are implemented as moving actions through motor commands.

Thus, in addition to the movement of the surrounding objects and the modulation related to the 3D structure of the surrounding environment, optic flow now results from a compound of eye movements in the head, head rotation relative to the body, and body motion in the environment. A critical issue for the navigator is the intrinsic ambiguity of this highly dynamic visual signal: with this, how to identify what is related to the external world (allothetic information) and what is related to the different components of self-motion (idiothetic information)? In the first following section, we will see that the cerebellum could be a key structure to disentangle these two types of information.

A supplementary difficulty is the reference frame in which can be coded those two type of information. A reference frame corresponds to the system of coordinates in which any space-dependent signal is coded into the brain. When the observer is static all reference frames are confounded, but when the observer is moving, we can distinguish two reference frames at least: one centered on the observer (egocentric) and one centered on the world (allocentric). Concretely, as the head and eyes can move as well, we may consider as many reference frames as there are mobile body parts. It is crucial then to distinguish the reference frame in which is coded a spatial signal, from the type of information conveyed by this signal (Arleo and Rondi-Reig, 2007). This can be sensory inputs on one hand, motor command on the other hand, but also any intermediate stage of processed information such as self-motion information,

and external cues extracted from the integrated sensory inputs, or a spatial representation combining idiothetic and allothetic information.

In the second section, we will see that identifying the type of information used by the navigator is essential to characterize a navigation behavior. This can be assessed through experimental manipulation: make one information available or not. The type of sensory input (visual, olfactory, auditory...) may also be manipulated. In all cases, the behavior, successful or not, will be a possible read-out. In contrast with this, the reference frame concerns a hidden variable of brain coding: assessing the reference frame in which is coded one information type requires to directly monitor the coding signal while the observer's location changes (Wolbers and Wiener, 2014).

In the same way it was important to disambiguate the words 'visual motion' and disentangle 2D retinal motion from perceived 3D motion as two different processing stages, it is now important to clearly identify what is related to sensory modality (visual, vestibular, auditory...) vs. information type (idiothetic, allothetic) vs. internal reference frames (Figure 23) ... I will try my best !

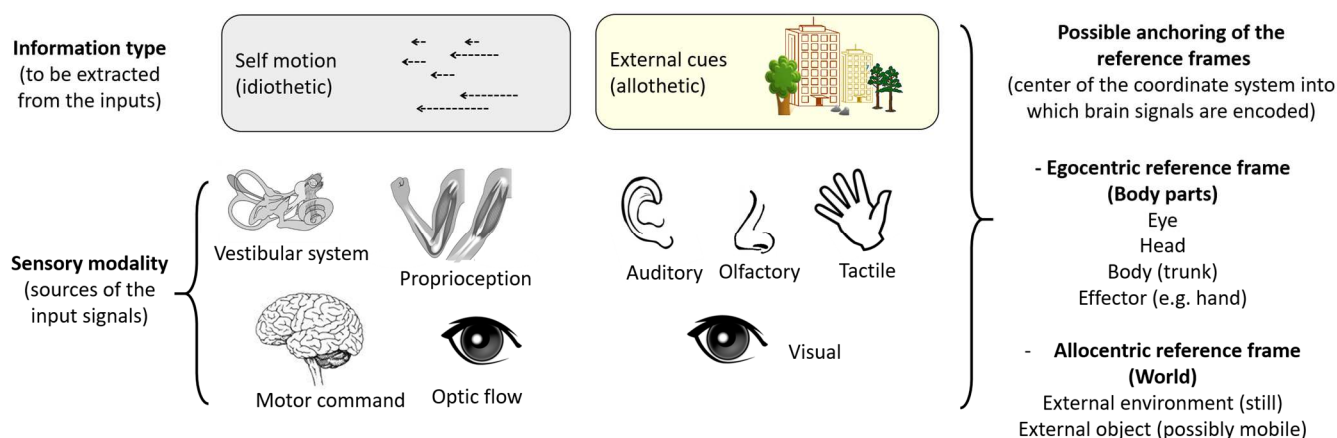


Figure 23. Sensory modality, information type and reference frames. As the 3D motion and form of the visual objects had to be extracted from the 2D retinal motion, idiothetic and allothetic information have to be extracted from the multi-modal inputs provided by our sensors. In the case of a moving observer, all brain signals –either raw signals from the sensors or processed information already integrated from multiple sensors– can be encoded into different systems of coordinates (reference frames).

Publication: [Review] Rondi-Reig L, Paradis A-L, Lefort JM, Babayan BM & Tobin C (2014) How the cerebellum may monitor sensory information for spatial representation. Front syst neurosci 8 (attached in Annexes) <http://dx.doi.org/10.3389/fnsys.2014.00205>

Our hypothesis is that the cerebellum monitors the sensory inputs to segregate the component resulting from our voluntary actions from that signaling novelty in the environment. The objectives of this review were to show that the cerebellum is adequately wired to integrate self-motion information from multisensory inputs; that the models of cerebellar computation allow to disentangle self-related from world-related information thanks to sensory prediction; and that the cerebellar output could contribute to update the activity of space-coding structures.

Multimodal integration

We focused our review on the vestibulo-cerebellum (flocculus/paraflocculus and their vermal counterpart here extended to lobules IX-X). We also included lobules of the posterior part of the cerebellum which have been found involved in cognitive functions, namely hemispheric lobules Crus I, Crus II and the vermal lobule VII.

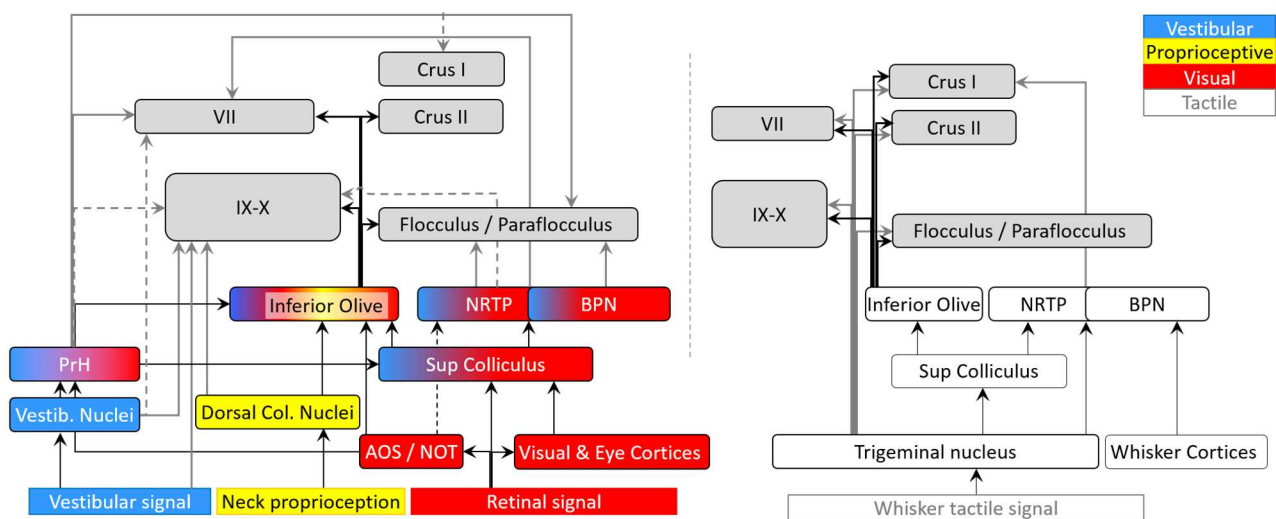


Figure 24. The cerebellum receives multimodal information. Anatomical projections of sensory inputs described in rodents and rabbits. AOS= Accessory Optic System; NOT= Nucleus of the Optic Tract; BPN= Basilar Pontine Nuclei; NRTP= Nucleus Reticularis Tegmenti pontis; PrH= Prepositus Hypoglossi Nucleus. Adapted from Rondi-Reig et al., 2014.

Figure 24 summarizes the vestibular, neck proprioception, visual and (whisker) tactile inputs that were found to project on our cerebellar lobules of interest. We can note that the different inputs initially follow separate pathways but may converge on common structures before reaching the cerebellar cortex. The superior colliculus thus integrates visuo-vestibular inputs and also receives tactile whisker signal.

In addition to visual, vestibular and tactile signals, the pontine nuclei (see BPN in Figure 24) has been shown to receive motor efferent copy, which is a copy of the motor command sent by the cortex to an effector. The convergence of sensory signals with the efferent copy is a crucial element that allows the cerebellum to make the distinction between voluntarily generated self-motion ('reafference' in Figure 25) and externally-driven sensory variations ('exafference').

Sensory prediction

Computational models of the cerebellum describe the cerebellum as an adaptive filter working in two stages: from the multisensory and motor signals integrated at the level of granule cells, relevant

components of the signal such as those related to self-motion information could be extracted through adaptive weighting between parallel fibers and Purkinje cells; the sensory signal to come would then be predicted through filtering at the output of Purkinje cells. By comparing sensory prediction with the actual sensory signal, likely at the level of deep cerebellar nuclei, the cerebellum provides an output that could be used to signal novelty arising from the environment (Figure 25) to forebrain structures (Figure 26).

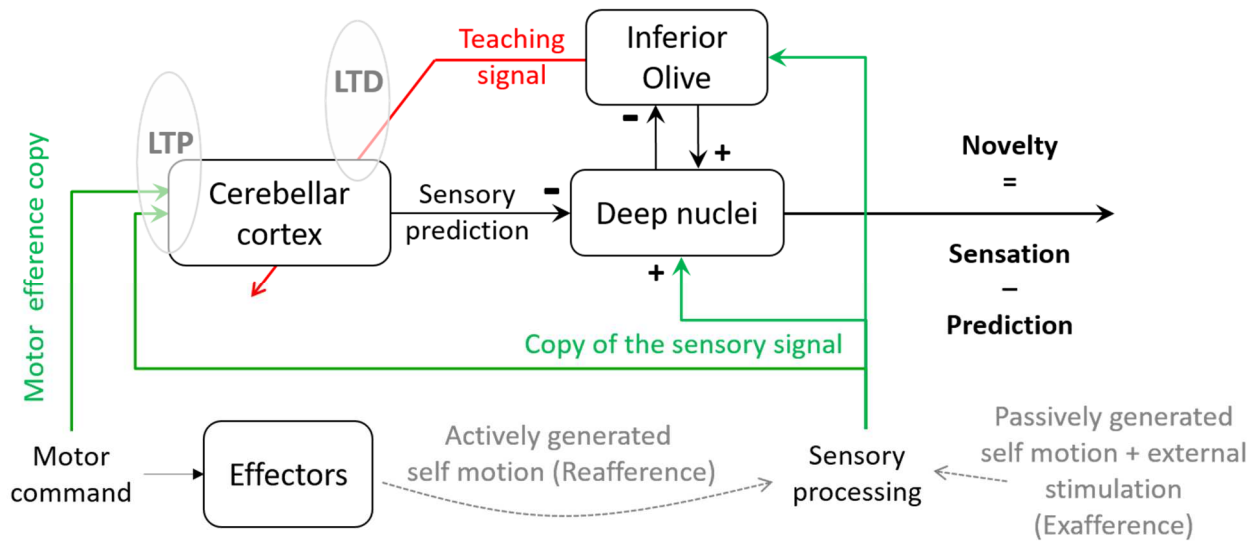


Figure 25. Schematic of the cerebellar computation. The cerebellum is commonly described as an adaptive filter: input signals could be integrated at level of the cerebellar cortex and transformed into sensory prediction sent to the deep nuclei. The weights applied to these inputs at the junction between parallel fibers and Purkinje cells are likely acquired through unsupervised learning implemented by LTP, and updated by LTD under the supervision of a teaching signal sent by the inferior olive through the climbing fibers, when the sensory prediction repeatedly differs from the actual sensory signal. Adapted from Rondi-Reig et al., 2014.

Interaction with space-coding structures

Depending on the computing lobules, the output signal could be sent to space-coding structures through two potential pathways (Figure 26): Lobule IX-X-flocculus and paraflocculus project to vestibular nuclei and PrH which directly feed the head-direction (HD) system where cells code for the head direction in an allocentric reference frame i.e. with respect to the external world; Lobules VII, Crus I and Crus II project through the deep cerebellar nuclei and ventro and centro-lateral thalamus to the parietal cortex where cells coding for self-motion direction and velocity in an egocentric reference frame have been described in rodents.

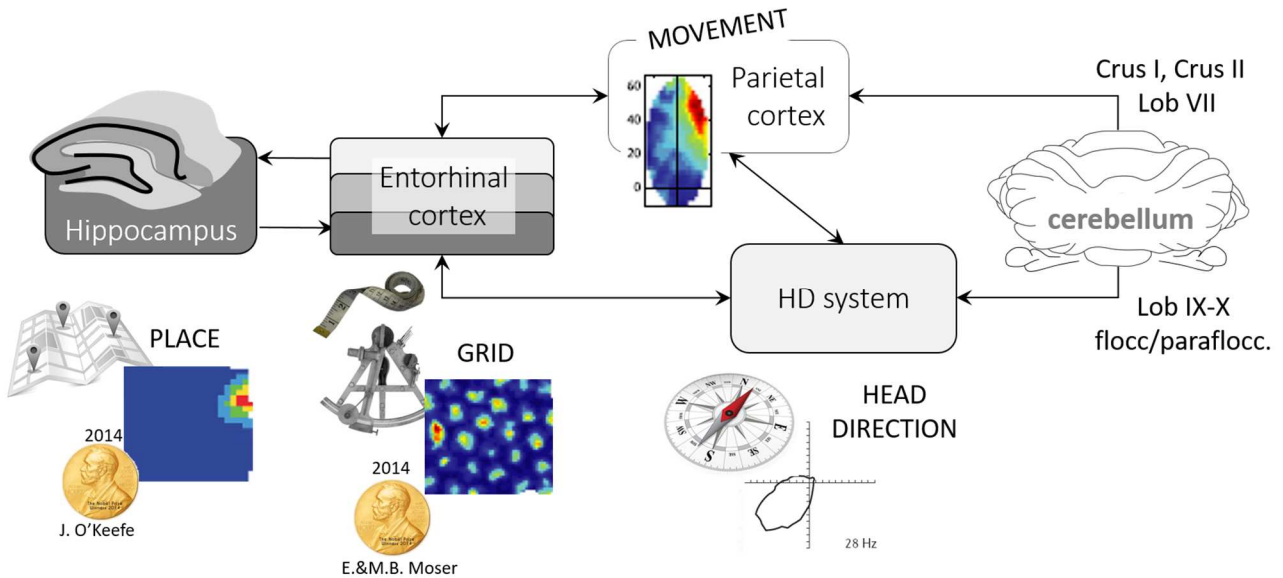


Figure 26. Cerebellar projections toward the navigation structures. Adapted from Rondi-Reig et al., 2014.

Through these two pathways, the cerebellum could thus influence both allocentric orientation coding and egocentric action planning, up to the hippocampal representation when pursuing downstream.

On one hand, the convergence toward the hippocampus supports the possible contribution of the cerebellum in updating self-orientation with respect to the internal map. This is in line with the results of Rochefort et al., 2011 showing that a genetic deficit of cerebellar LTD impaired place cell activity when self-motion information was mandatory to perform the navigation task. On the other hand, the double path suggests that the cerebellum may play different roles depending on the type of representation used to navigate, and specifically the reference frame on which it is anchored. The study presented in the next section thus raises the question of how the cerebellum is activated depending on whether the navigator uses a strategy based on egocentric action movements made at successive choice points or on a *supposedly* allocentric representation of the environment.

In practice, the use of an internal representation of the environment is particularly required when the goal of the navigation is not directly visible, so that navigation relies on memory: memory of the place configuration around the goal (Figure 27A) and/or memory of the way to reach it (B and C). Although depending on memory, the ‘simple’ egocentric strategy is not considered to depend on the hippocampal representation of space. By contrast with this, the sequence-based strategy, which requires to memorize a series of actions organized in space and time, has been proved to depend on the hippocampus in mice (Rondi-Reig, 2006). In humans, this strategy has been shown to induce BOLD activation in the hippocampus, as did the use of a place-based strategy (Iglói et al., 2010). Moreover, the study revealed that the human hippocampal activation was lateralized: on the left when the participants used sequence-based strategy, and on the right for the place-based strategy.

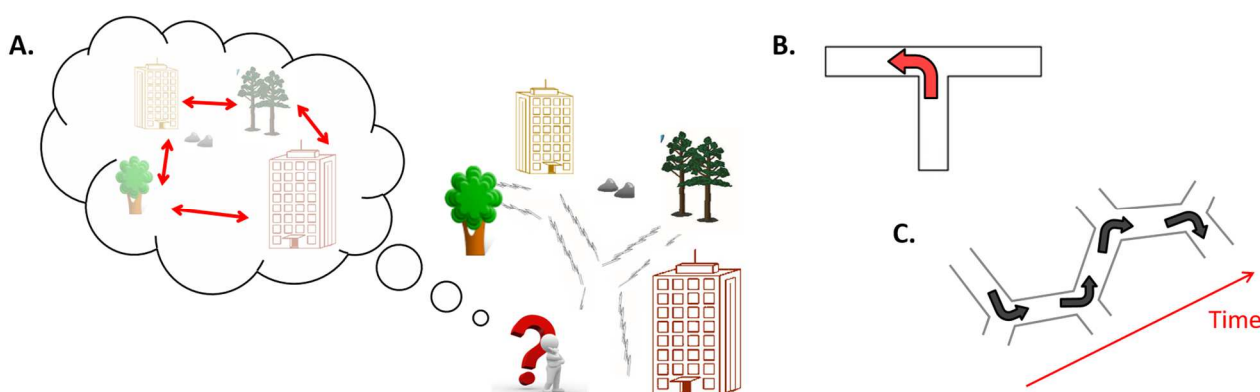


Figure 27. Navigation strategies based on memory. (A) ‘Place-based’ or ‘Map-based’ strategy: the navigator self-localizes and self-oriens with respect to the external world, relying on stored relationships between external landmarks (spatial memory). (B) ‘(Simple) Egocentric’ strategy: the navigator learns to associate a response action to a given stimulus—here, turn left at the intersection (procedural memory). (C) ‘Sequential Egocentric’ or ‘Sequence-based’ strategy: the navigator has to learn a sequence of self-movements organized both in space and time.

With the hypotheses presented in the previous section, the question then was: how the cerebellum may intervene in two strategies which both rely on the hippocampus but differentially depend on idiothetic and allothetic information, and are thought to anchor onto different reference frames (Arleo and Rondi-Reig, 2007).

Sequence-based vs. place-based navigation

Publication: Iglói K, Doeller CF, Paradis AL, Benchenane K, Berthoz A, Burgess N & Rondi-Reig L (2015). Interaction Between Hippocampus and Cerebellum Crus I in Sequence-Based but not Place-Based Navigation. Cerebral Cortex 25(11): 4146-54. Epub 2014 Jun 19 (attached in Annexes) <http://dx.doi.org/10.1093/cercor/bhu132>.

This second study, based on the same data as Iglói et al. (2010), was aimed at specifying the implication of the cerebellum in a complex navigation task, depending on whether the strategy to reach the goal was based on place identification or sequence reproduction. Both activity and functional connectivity were studied.

The results reveal that the two strategies rely on complementary networks, which were activated together during the training phase (Figure 28 A,B and C). For each strategy, we found lateralized cerebellar activity contralateral to the hippocampal activity previously described. In both cases, the activated lobule compared to the control condition was Crus I (Figure 28 B and C). Consistently with what could be expected from the hypotheses based on the review, lobules IX-X were more activated for the place-based strategy compared to the sequence-based strategy. Note that these lobules were also highlighted as part

of the sensory-motor network which was commonly activated by all the navigation conditions (Figure 28D), likely because visuo-vestibular information is continuously processed in all these conditions.

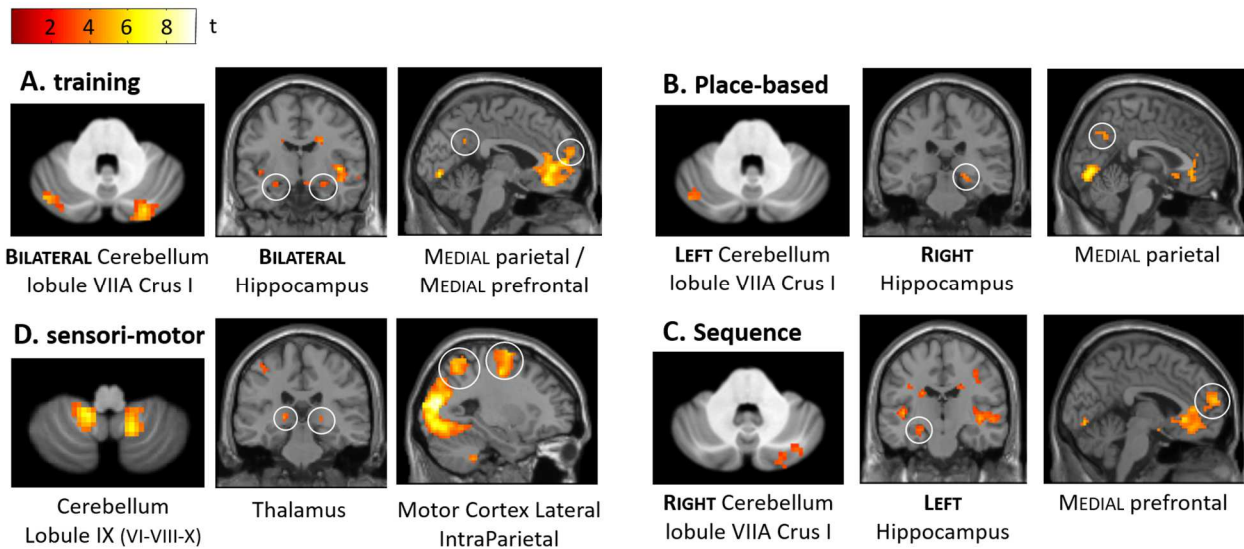


Figure 28. BOLD activity related to training (A), place-based or sequence-based (C) navigation, or generic sensory-motor activity (D). To allow comparison between the different navigation conditions, the analyses were limited to the first alley of the maze. The figure D illustrates the activation of lobule IX, but lobules VI-VIII-X were found activated as well. Adapted from Iglói et al., 2015.

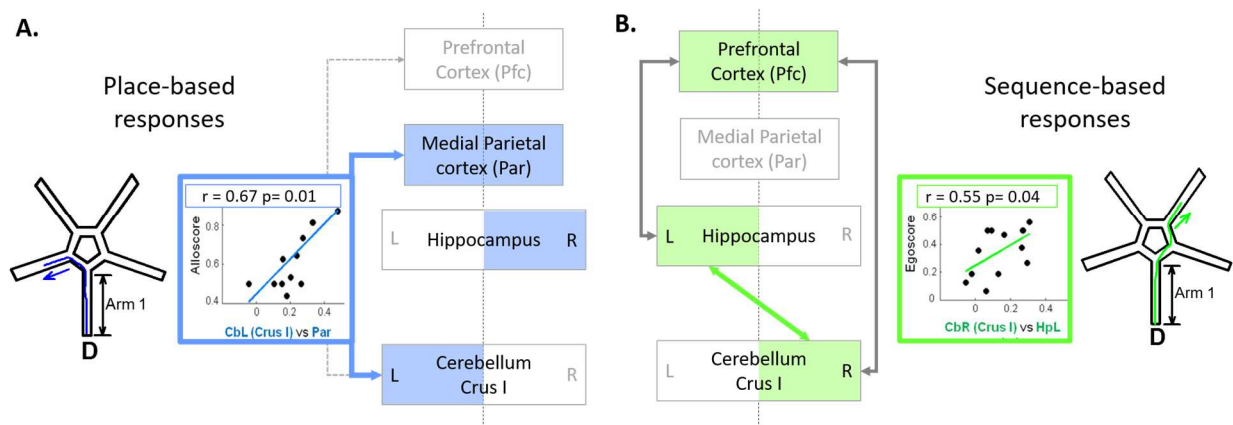


Figure 29. Navigation networks subserving the place-based (A) and sequence-based (B) strategies. Blue (resp. green) boxes correspond to areas activated in place-based (resp. sequence-based) responses. Solid connecting arrows indicate significant functional connectivity ($r > 0.18$) between the activated structures. Colored arrows further indicate a significant positive correlation between the functional connection strength and a score (see alloscore/egocore in the insert) measuring the tendency of the participants to use the considered navigation strategy. The dotted grey arrow in A indicates that a positive correlation was found between the tendency to use the place-based strategy and the level of functional connectivity between the left cerebellum and the medial prefrontal cortex, although this latter was not found significantly activated during the place-based responses. Adapted from Iglói et al., 2015.

Functional connectivity analysis

Functional connectivity analyses further revealed coupling between the cerebellum and specific structures of interest depending on the strategy. For the place-based strategy, the activity of the left cerebellar Crus I was significantly correlated with that of the medial parietal cortex (precuneus). For the sequence-based strategy, significant correlation was found between the right cerebellar Crus I and the left hippocampus. In addition, the strength of these functional connections were themselves correlated

with the tendency of the participants to use the corresponding strategy (colored arrows in Figure 29), further suggesting the importance of the functional connections in the observed behavior.

For the place-based strategy, the coordinated activity of the cerebellum Crus I with the medial parietal cortex (precuneus) is consistent with the described projections of this lobule toward the parietal cortex. The context of activation (place-based strategy) may seem at odds with the supposed role of this pathway in egocentric action planning, unless we consider that egocentric action planning has to be performed whatever the strategy. In this case, such planning may require supplementary processing (coordinate transformation) when the spatial information used to self-localize is coded in an allocentric reference frame.

As for the hippocampus, it was active during the planning of the trajectory in the first alley, but its activity was not coordinated with that of the cerebellum. This is consistent with the proposal of Spiers and Maguire that the hippocampus is briefly involved at the initiation of the behavior to plan the routes to specified goals, but does not sustain the behavior along the trajectory (Spiers and Maguire, 2006). This was also consistent with our observation that the hippocampal activity was not sustained in the following alleys of the maze. This could be mean that, for the place-based strategy, planning occurs only once at the beginning of the trial.

In contrast with place-based strategy, the activity of the left hippocampus was coordinated with that of the cerebellum Crus I for the sequence-based strategy along the first alley. Moreover, complementary analyses suggested that the hippocampus activity was sustained beyond the first alley. How can this be consistent with the view that the hippocampus only discretely participates in route planning? Maybe if we consider that sequence-based strategy requires new route planning at each decision point of the trajectory. Note that this would also be in agreement with the involvement of the prefrontal cortex in this strategy. The seemingly sustained fMRI activity would then correspond to repeated reactivations of the hippocampus. However, brain recording with better temporal resolution would be necessary to clarify this point.

With this experiment, as distal landmarks were always present, we cannot completely exclude that hippocampal activity observed in sequence-based strategy be related the coding of this allothetic information and/or an automatic update of the spatial map. The following study aimed at eliminating this possible confound and determine which structures are involved in sequence-based navigation when the trajectory is learned in an impoverished environment so that only self-motion can inform the behavior.

Sequence learning from self-motion

PhD work of B Babayan supervised by L Rondi-Reig in collaboration with B Girard (ISIR)

In this study, mice were trained to swim in a double Y-maze where all possible distant landmarks were masked by a black circular curtain surrounding the maze. The goal of the task was to find a platform hidden under the water surface. The platform was always located at the same place and the mice always started from the same departure point. To reach the goal they thus had to learn a fixed sequence of two body turns (left then right). Mice underwent 4 sessions of 4 trials per day, for a maximum of 5 days until they reached the 'learning' criterion (Figure 30B). The last day they were sacrificed to reveal the c-fos expression related to their behavior.

C-fos activity in sequence-based navigation

C-fos density was measured in 34 regions of interest (Figure 30A) including hippocampus, cerebellum, cortical structures and basal ganglia. Among 30 trained mice, 15 were able to reach the learning criterion in less than 6 days. To control for the c-fos activity related to motor activity, the c-fos activity of the test mice was normalized and compared to the activity of paired control. Those control mice were left to swim in a reduced version of the maze (two arms only, no platform) for the same duration as their paired test

mice: as the test mice learned the sequence (Figure 30C), their controls were left to swim for a shorter duration. Figure 30D illustrates among the counted regions which were significantly more activated in mice having learned the sequence compared to the swimming controls.

The activated regions included the parietal cortex (Par, PostPar) and the granular retrosplenial cortex (RSG), both associated with reference frame manipulation or egocentric motion coding; the DMS, crucial to perform goal-directed navigation (Fouquet et al., 2013); three hippocampal regions (dCA1, dCA3 and vCA3) as well as posterior lobules of the cerebellum (Lob VI, VII and CrusI) along with the deep nuclei which correspond to the output of the cerebellum. By contrast, the entorhinal cortex was not found more activated than in control mice.

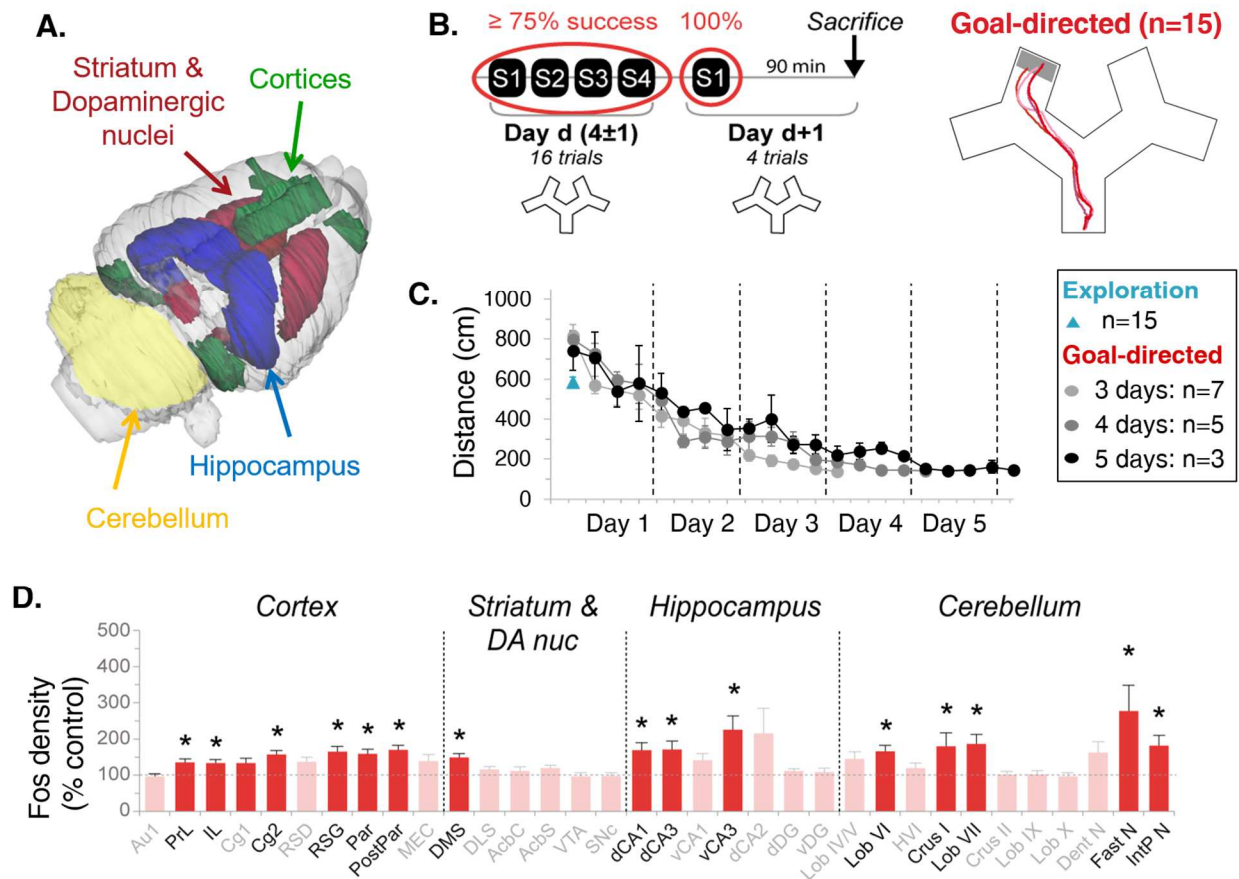


Figure 30. Activation subserving goal-directed sequence-based navigation. (A) Localization of the 34 regions of interest analyzed for *c-fos* activity. (B) Learning criterion: successful mice were able to perform at least 75% of direct paths in a 16 trials session in less than 6 days, then perform 100% direct paths in a 4-trial session the following day. On the right, examples of trajectories performed the last day (d+1), once the sequence corresponding to a successful goal-directed navigation was learned. (C) Average learning curves of the mice having reached the learning criterion. Efficient goal-directed navigation was acquired in 3, 4 or 5 days depending on the mice. (D) *c-Fos* positive cell densities for the mice having reached the learning criterion, normalized with respect to controls paired in swimming time. *Mann-Whitney $p < 0.05$ for comparison to swimming control group.

Learning models

To further focus on the process sustaining sequence learning, the actual learning curves of the mice were compared to that simulated with three classical models of spatial learning: model-based and model-free reinforcement learning and path integration. The model of path integration consists in monitoring self-movement to update self-position with respect to the departure point. Model-based reinforcement learning is the choice model for goal-directed navigation involving the hippocampus since it allows to simulate/anticipate the trajectory up to the goal once the learning achieved. In contrast, model-free reinforcement learning is based on stimulus-response association (Figure 31) and is most often associated

with simple egocentric strategies. In the case of a sequence of actions however, it has been proposed that learning could rely on chained stimulus-response associations.

In our case, the landmark were purposely minimal so that a stimulus limited to a local description of the maze offered no way to distinguish between two successive intersections. Such situation was incompatible with an efficient learning that requires to associate two distinct actions at two seemingly identical intersections (Figure 31C). The only way to make the learning possible with stimulus-response association was thus to introduce supplementary information into the stimulus definition. The most relevant information being self-motion, this was done by introducing a memory of the last (three) actions. With this, it becomes possible to make the distinction between two seemingly identical intersections: For example, the first intersection encountered after going straight forward from the departure point, and the second intersection encountered after turning left once (Figure 31D).

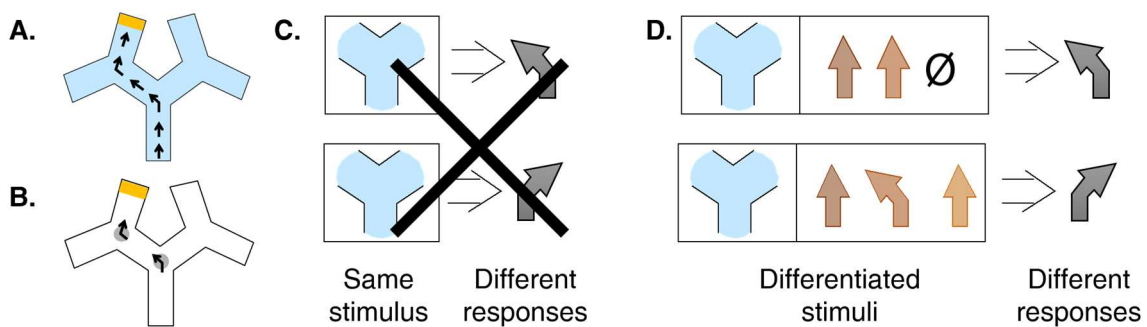


Figure 31. Learning model based on stimulus-response association. (A) Trajectory to be learned. (B) Critical decision points to learn the sequence; note that different response actions are expected at those successive decision points (left turn first, right turn then). (C) Based on allothetic information, the stimulus is the same at the two successive decision points, which does not allow to learn different response actions. (D) Including a memory of the last past actions to the 'stimulus' allows to differentiate the context at the critical points so that it becomes possible to learn to produce different actions at those decisions points.

Rather surprisingly, it was the model-free reinforcement learning with past actions that best fitted the learning results of the real mice in terms of learning dynamics. In contrast, the learning curve of the model-based and path integration were too steep compared to the smooth evolution of the real curve (Figure 30C). We thus obtained for each mouse individual learning parameters corresponding to the parameters of the model that fitted its learning curve best.

Correlation of c-fos activity with learning

In a second step, we tested the correlation of these learning parameters with the c-fos activity of each region. Note that this approach relies on a variability of the c-fos expression between mice. This variability however cannot be explained by the performance in the sequence-based task since the final performances were equalized by the use of the learning criterion. Our hypothesis is that this variability can be explained by different learning dynamics.

Figure 32 (left) illustrates the significant correlations observed for the learning parameter β . This parameter represents the exploration/exploitation trade off, i.e. to what extent a mouse tends to apply the same learned trajectory each time (learning exploitation) or starts to explore its environment again.

Among all the tested structures, only hippocampal and cerebellar subregions were found significantly correlated with the β parameter. This result confirms the central role of this two structures in sequence learning even in the absence of visible landmarks. Moreover, this result suggests a specific role of CA3 and the deep cerebellar nuclei in choosing to learn more about the environment or apply the sequence already learned.

Connectome analysis

Lastly, a ‘connectome’ analysis was performed to reveal which areas were co-activated (Figure 32 right). This analysis relied on computing matrices of correlation between all couples of regions across mice. This approach is very similar to functional connectivity computed in fMRI, except that with one value per mice the correlation is based on inter-individual comparison. A clustering analysis performed on these correlation matrices revealed subsets of regions working together, and further identify dCA1 and a cerebellar cortical lobule as ‘hub’ regions.

Hubs are characterized by a great number of connections with the rest of the network and the fact that they participate in a maximum number of short paths between regions. Finding dCA1 as a hub for sequence-based navigation and CA3 correlated with a learning parameter is consistent with the view that CA3 could provide memory information to CA1 (Cabral et al., 2014) which would in turn serve as an interface with other brain structures.

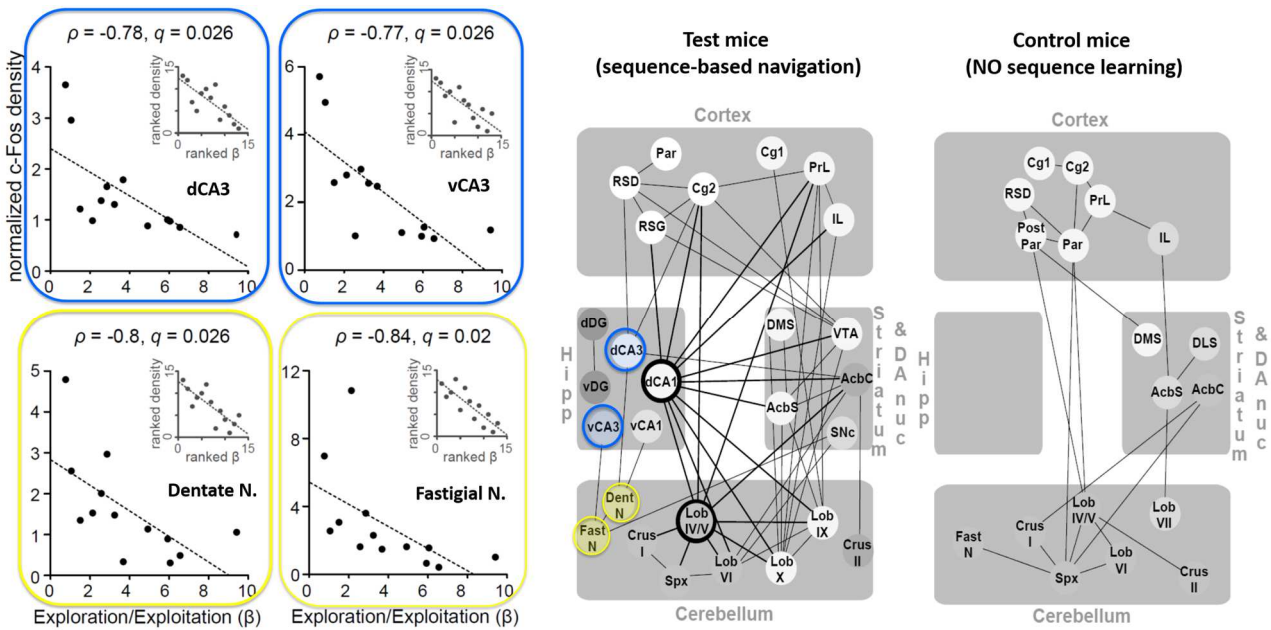


Figure 32. Correlation analyses. (Left) Significant correlation between c-fos activity measured once the task was acquired and the β parameter of the best learning model. Yellow is for cerebellar regions, blue for hippocampal regions. β corresponds to the exploration/exploitation trade-off. q : FDR-corrected p -value. (Right) Connectome analysis based on the correlations between all pairs of regions. Regions highlighted with a black circle were characterized as hubs of the network. Regions highlighted in color displayed activity correlated with the learning parameter β .

Discussion

The connectivity pattern revealing co-activation of the cerebellum and the hippocampus confirms that the functional connectivity observed in fMRI did not only reflect the updating of external landmarks with respect to self-motion. Instead, the hippocampus appears truly involved in the performance of sequence-based navigation even in absence of landmarks.

More surprising, the best fitting model did not correspond to a model-based learning algorithm as initially expected. Instead, it corresponded to model-free reinforcement learning with a memory of the past actions. The introduction of a memory of past actions also modifies the way the internal state is encoded in the learning model. Strictly speaking this does not affect the fact that the algorithm does not explicitly model the transitions between states and thus cannot simulate a trajectory and make prediction about the possible outcome of this behavior. However, the stimulus cannot be considered as allothetic information anymore, and gains a dynamic dimension (succession of actions). In addition, implicit priors are added to the representation of the ‘world’ (e.g. actions are ordered in time).

Overall, this result raises questions about the way such model could be implemented with the brain areas highlighted here. Indeed, model-free learning has been proposed to be implemented by the DLS in association with the hippocampus to provide the contextual spatial state (Khamassi and Humphries, 2012).

Here, the hippocampus could still provide a contextual state but rather temporal than spatial since including the memory of the past actions. This would be consistent with the view of Eichenbaum, who proposed that the role of the hippocampus in navigation is to provide memory whether it is spatial or not (Eichenbaum, 2017).

What would be the role of the cerebellum then? One interpretation is still that the cerebellum processes sensory inputs and provides self-motion information to the hippocampus. With the results obtained here, this self-motion information could be sent to dCA3, maybe through the parietal and retrosplenial cortices which are part of the same cluster as dCA3. The hippocampus dCA1 could then receive memory information from dCA3 CA1 (Cabral et al., 2014) to implement the internal representation of the contextual information mandatory to perform the task (i.e. the combination of actual state and past actions provided by CA3).

Although this study provided a more precise view of the sub-regions involved in sequence learning (in the hippocampus and cerebellum particularly), it also raises more questions about the direction of information exchange between those structures. Only electrophysiological recording with high temporal resolution may help clarify this point.

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With the previous studies, we saw that the notion of egocentric and allocentric reference frames is quite complex. To end with this review of my previous work, I will come back to an older work (from a time I did not know about the cerebellum yet...). The aim of this study was precisely to determine the brain areas sustaining the processing of visual inputs into different spatial reference frames and the ability to use those different reference frames to analyze distance information.

Participants had to judge the relative distance of two objects in three conditions, each corresponding to a specific reference frame: the distance could be estimated with respect to themselves (viewer-centered reference frame), with respect to a third mobile object (object-centered) or with respect to a fixed element of the landscape (landmark-centered). A fourth non-spatial task was used as control (Figure 33). Comparisons were made between the activation related to each spatial task and the control task (Figure 34), as well as between spatial tasks.

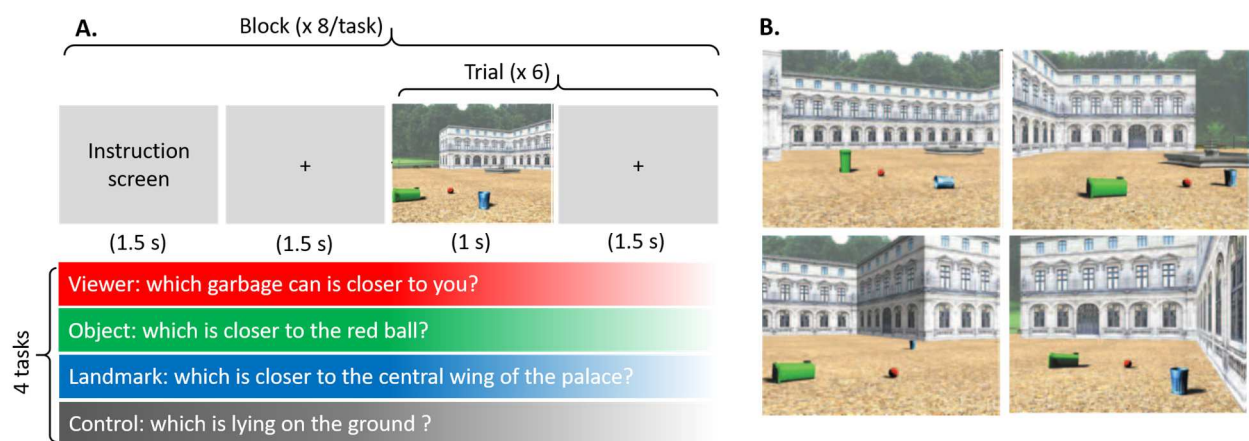


Figure 33. Experimental protocol. (A) Fourteen participants underwent a total of 32 blocks of 6 trials each. (B) Examples of viewpoints among the possible twelve. At each viewpoint, four images with different object configuration were created, for a total of 48 stimuli distributed into 6 trials x 8 blocks for each task.

Posterior parietal cortex

Common activation was found for the three spatial tasks in the posterior parietal cortex extending to the superior/middle occipital cortex (bilateral regions 1 and 2 in Figure 34). Although the posterior parietal cortex has been associated with egocentric coding of space with respect to various body parts, and sometimes found involved in spatial perception or judgments based on objects, less results support the contribution of the posterior parietal cortex to world-centered coding. Taking into account the data available at that time as well as more recent studies, different parietal areas appear to code visual target location (Snyder et al., 1998) and vestibular signals (Chen et al., 2013) into different reference frames.

For example, area 7a located in the inferior parietal lobule, was found to code visual information in retina- as well as object-centered or world-centered coordinates and could implement the transformation from one reference frame to another (Crowe et al., 2008; Snyder et al., 1998). VIP along the intraparietal sulcus was found to integrate vestibular, visual and tactile signals in body- or world-centered coordinates. It has been proposed to sustain multisensory representations of peripersonal space for the perception of self-movements and object movements in this space. In contrast with these, LIP appears to code visual target location in body-centered coordinates only (Snyder et al., 1998) and would be involved in coding

saccadic movements. MSTd in turn rather codes vestibular signals and optic flow in eye-centered to head-centered coordinates (Chen et al., 2013), and could contribute to perceive heading direction.

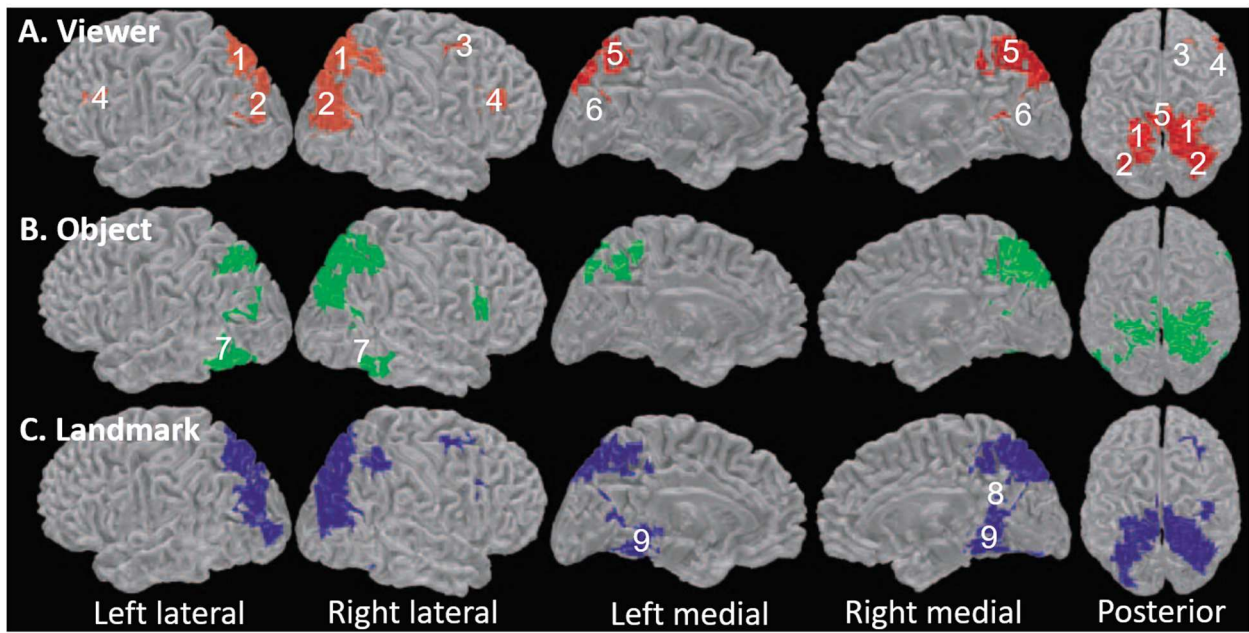


Figure 34. Activation relative to the control task for viewer-centered (A), object-centered (B) and landmark-centered (C) location judgments. 1=superior parietal lobule, 2=superior and middle occipital gyri, 3=superior frontal sulcus/superior precentral sulcus (frontal eye fields), 4=inferior frontal sulcus/inferior precentral sulcus, 5=dorsal precuneus, 6=parietal–occipital sulcus, 7=lateral occipital–temporal (LOC, pFs), 8=posterior cingulate (retrosplenial), 9=medial occipital–temporal (fusiform, lingual, and posterior parahippocampal gyrus); adapted from Committeri et al., 2004.

Szczepanski and Saalman then suggested that the numerous sub-regions of the parietal cortex could participate in parallel pathways, each coding spatial information in a coordinate system specifically adapted to the supported behavior e.g. eye-centered system for gaze or attention orientation, hand-centered for grasping movements, head-centered for heading perception, world-centered for some navigation tasks, and object-centered when flexible spatial representations are required, as in task switching conditions... (Szczepanski and Saalman, 2013). The authors further proposed that the parietal cortex may represent behavioral priorities in multiple reference frames including more abstract spaces, such as numerical space. Note that, if we extend this notion to the feature space, it is fully consistent with the previous proposal that parietal activity might be involved in selecting –or suppressing– visual features relevant –resp. irrelevant– to the task (Liu et al., 2012; Mevorach et al., 2009).

Medial occipito-temporal cortex

Overall, three main regions were found more activated for the landmark-centered task compared to the other two. The superior parietal lobule, the medial occipito-temporal cortex and the medial parietal cortex, including the retrosplenial cortex and the precuneus. Our proposal at that time was that the simultaneous activity of these areas mainly reflected the mental matching between a stored representation of the environment (previously visited from a route perspective) and the current viewpoint on the environment.

The areas highlighted in the ventromedial temporal lobe are part of the ventral visual pathway. As such probably, they probably show increasing invariance with respect to the retinotopic position of the considered visual object, or the observers’s viewpoint, and thus likely contribute to code information in an allocentric reference frame.

Medial parietal cortex: retrosplenial cortex and precuneus

The Retrosplenial cortex has been proposed as the 'transition zone between egocentric and allocentric representations' (Aguirre and D'Esposito, 1999). Its role could be to compute translations from one reference frame to the other. By changing viewpoint at each trial, all tasks reorient the participants in the environment at each time. However, only the landmark-centered task requires that the participants anchor their representation to the external landmarks and reorient themselves to correctly perform the task. Retrosplenial might perform a comparison between the currently perceived environment (in local self-centered view) with a stored allocentric representation of the environment and thus 'anchor' the representation with respect to the current view (Cabral et al., 2014; Marchette et al., 2014) or reciprocally encode head direction in the allocentric reference frame (Shine et al., 2016).

The precuneus had been previously found related to memory and imagery processes, especially after mental navigation in an environment learned from a route perspective (which was the case here). Then it might contribute to build and use a representation of the environment from an egocentric perspective. This view is consistent with recent findings showing that the precuneus represents the direction to the goal in an egocentric reference frame (Chadwick et al., 2015).

Altogether the retrosplenial and precuneus might translate the current viewpoint into landmark-centered information. In navigation conditions, it might reciprocally translate an allocentric representation of the environment into egocentric goal directions.

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SUPERVISED MASTER AND PHD WORK

PhD *(co-supervision)

Nadine Francis. *Cerebellum-forebrain interaction for navigation in humans.* UPMC – Paris 6. 2nd year. *(L. Rondi-Reig).

Frédéric Benmussa. *Reconnaissance d'objets naturels et marquage fréquentiel en MEG.* UPMC – Paris 6. Defended on July 16, 2013. *(J. Lorenceau)

Ying Liu. *Visual consciousness and its relation with feature-based attention: behavioral experiments and magnetoencephalographic recordings in humans.* UPMC – Paris 6. Defended on Oct 22, 2012. *(C. Tallon-Baudry)

Agnieszka Miskiewicz. *Interactions entre mouvement et forme lors de la reconnaissance d'objets 3D dynamiques : comportement et bases neurales.* UPMC – Paris 6. Defended on Feb 6, 2009. *(J. Lorenceau)

Master

Bérenger Thomas (2016), *Évaluation des capacités de navigation spatiale chez des patients autistes.* M2 Biologie Intégrative, UPMC – Paris 6 *(L. Rondi-Reig)

Nicolas Traut (2015), *Cervelet et autisme.* M2 Bioinformatique et Modélisation (BIM), UPMC – Paris 6 *(co-supervision and collaboration with R. Toro, A. Beggiato, institut Pasteur)

Daphné Silvestre (2014), *Bases neurales de la mémoire spatio-temporelle chez l'Homme.* M2 BIP, UPMC *(L. Rondi-Reig)

Laura Benhaïm (2010). *Évaluation d'un protocole de test de suivi de l'amblyopie fonctionnelle de l'adulte : une première approche chez des sujets sains.* Master Rééducation et Ingénierie Médicale, Spécialité recherche clinique, UPMC – Paris 6. *(J. Lorenceau)

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Fabrice Clair (2004) *Vers la construction d'un système générique pour la détection automatique d'artefacts sur signaux MEG et EEG.* DEA d'imagerie médicale, Paris 11. *(J.B. Poline)

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Peer-reviewed conference papers

20. Miskiewicz A, Buffat S, Lorenceau J & Paradis A-L (2010) *Temporal dissection of stimulus-driven and task-driven processes during perceptual decision about 3D SFM stimuli*. S. Supek and A. Sušac (Eds): Advances in Biomagnetism – BIOMAG2010, IFBME Proceedings, 28: 326-329. http://dx.doi.org/10.1007/978-3-642-12197-5_76
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Invited papers

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23. Cornilleau-Pérès V, Paradis A-L, Droulez J (1998). Visual Perception of 3D shape from motion: multisensory integration and cortical bases in: Vision and Action, LR Harris and M Jenkins (Eds.) Cambridge University Press, pp 231-249.

License deposits

- Deposit of the "Virtual Starmaze" to the French Program Protection Agency (APP), July 20, 2016 (IDDN.FR.001.340006.000.S.P.2016.000.10000)
- Deposit request for "NAT-h" in progress (contributors: L Rondi-Reig, AL Paradis, G Sedes, A Greiner)

Résumé

Les indices visuels de mouvement donnent accès à trois types d'information : le mouvement propre, le mouvement des objets environnants, et la structure de la scène visuelle elle-même. Je me suis d'abord intéressée à la façon dont le cerveau reconstruit la forme et le mouvement tridimensionnels des objets visuels à partir du champ de vitesses bidimensionnel qu'ils projettent sur la rétine. En étudiant le comportement et l'activité cérébrale, j'ai ensuite cherché des interactions possibles entre les informations de mouvement et forme, ainsi que le niveau de traitement auquel elles pourraient avoir lieu. De manière plus générale, j'ai exploré l'activité cérébrale liée aux processus d'intégration et sélection de deux caractéristiques visuelles d'un même objet. Dans un second temps, je me suis intéressée à la situation de l'observateur navigant. Outre la prise en compte du mouvement propre, les tâches de navigation complexes requièrent la mise en place et l'utilisation d'une représentation en mémoire de l'espace environnant et des trajets. Cette partie de mon travail porte ainsi sur les relations entre perception, action et mémoire spatio-temporelle.

Mots-clefs : perception visuelle, mouvement, forme, structure à partir du mouvement, cognition spatiale, mémoire, imagerie cérébrale fonctionnelle, IRMf, MEG, comportement

Abstract

Visual motion gives rise to three types of information: self-motion, the motion of surrounding objects, and the three-dimensional (3D) structure of the visual scene. I was first interested in how the brain reconstructs the 3D motion and form of visual objects from the two-dimensional velocity field they project onto the retina. I then studied behavior and brain activity to sight possible interactions between 3D motion and form, as well as their likely processing level. More generally, I explored the cerebral activity related to the integration and selection of two visual features from the same object. In a second phase, I got interested in the situation of a navigating observer. In addition to taking self-motion into account, complex navigation tasks require to build, maintain and utilize a stored representation of the our paths and surrounding environment. This part of my work thus focuses on the relationships between perception, action and spatio-temporal memory.

Key-words: visual perception, motion, shape, 3D structure from motion, spatial cognition, memory, functional brain imaging, fMRI, MEG, behavior