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Specificity of dorsal vs. ventral responses to 3D motion and form in passive viewing.

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ABSTRACT

We previously identified a number of regions that were selectively activated by transitions of 3D form and 3D motion attributes, either relevant or irrelevant to the task performed by the observers. Here, we tested the same areas with purely-passive viewing conditions. We hypothesized that the areas previously activated by unattended transitions should be activated by the same transitions viewed passively. Unexpectedly, although the occipito-temporal areas were consistently activated by the passively-viewed stimulus transitions, none of the dorsal areas presented any significant activity. Further, the selectivity for the 3D motion seems to disappear in passive viewing. Our results suggest that the dorsal areas considered here are activated by 3D motion in a task context only. The role of the dorsal pathway relative to 3D motion processing is revised in the light of the present results.

KEYWORDS

Structure from motion; 3D motion; 3D shape; dorsal pathway; ventral pathway; fMRI; passive viewing; stimulus-driven.

ABBREVIATIONS

3D = three-dimensional; SFM = Structure from motion; BOLD = Blood Oxygenation Level Dependent; (f)MRI = (functional) Magnetic Resonance Imaging; EPI = Echo Planar Imaging; ROI = Region of interest; LO = Lateral Occipital Area.

INTRODUCTION

Perceiving 3D moving objects implies identifying motion directions as well as recognizing shapes. With real-life objects, static cues are usually available to extract the global shape (e.g. local contours) so that brain activity related to the final shape perception can hardly be disentangled from brain activity related to the early processing of these visual cues. Using structure-from-motion (SFM) stimuli, for which the global form as well as the global motion are defined through motion cues only, it is possible to target the activity related to the end-percept 3D attribute while ignoring cue-dependent intermediate stages of processing. In a previous work using a factorial design that independently modulated the feature attended by the observer and the stimulus attributes, we were able to unveil a number of cortical areas selectively involved in processing 3D motion or 3D shape, for attention-related and/or stimulus-driven conditions (Paradis *et al.*, 2008). The stimulus-driven conditions consisted of 3D-motion or 3D-form transitions occurring while an incident task focused the observers' attention on the colour of the stimulus. In the present work, we wondered whether the same areas would be activated if similar modulations of the stimulus attributes were presented in purely passive viewing conditions. Our hypothesis was that the areas activated in our previous stimulus-driven condition would also be activated by passively-viewed changes, but that areas activated when attention was directed to the feature may not.

METHODS

Stimulation

Visual stimuli consisted of 200 coloured dots and a central fixation, displayed on a black background and viewed through a 16° diameter virtual window. There were 5 blocked conditions where the dots could be either static (ST: 10 blocks), moving incoherently (IM: 10 blocks) or moving coherently as if they belonged to a three-dimensional surface oscillating in depth (3D: 15 blocks). The 3D blocks were divided into 3 conditions of 5 blocks each, where the form of the stimulus, its 3D motion or its colour arrangement changed every 2 s., each time the oscillating surface passed through the central and initial position. As in Paradis *et al.* (2008), the 3D form alternated between a paraboloid and a horse-saddle; the oscillation axis tilted in the screen plane by an angle of 45°, 60° or 90°; and 85 to 95 % of the dots reversed colour (from red to green and vice versa). In the IM blocks, the direction of motion of all dots changed every 2 s by an angle comprised between 30° and 100°. Block durations varied from 4 to 12s, with the whole experiment lasting 5m 12s. In the scanner, stimuli were back-projected on a translucent screen that participants could see through mirror glasses. Participants were instructed to fixate a cross at the centre of the display.

Data

We analysed the data from ten healthy volunteers (4 men, 6 women) aged 21-28 years. All had normal vision; all but one were right handed, and one had a left ocular dominance. Functional data were acquired in a 3T whole body MRI system (Bruker, Germany), using a T2*-weighted gradient echo EPI sequence (flip angle 90°, TE = 40ms, TR = 2 s) sensitive to BOLD contrast, with 18 contiguous slices (in-plane resolution 3.75 x 3.75 mm², 6 mm thickness) covering the cerebral cortex, but excluding the cerebellum and the most inferior part of the temporal poles.

These data were acquired in the context of a more general study, which was approved by an Institutional Ethic Committee and was conducted with the understanding and written consent of each participant. In this context, participants underwent four runs of functional acquisition during the scanning session. In the last two runs, participants had to pay attention to the motion, form or colour of a 3D stimulus. The analysis of these runs was described in a previous work (Paradis *et al.*, 2008) and used to delineate the regions of interest for the present work. The passive-viewing data presented here were acquired during the first run in order to avoid a possible attentional bias toward one specific attribute of the stimulus.

Data analysis

Functional data were corrected for their geometric distortions and the first three scans acquired during the transition to the steady state of the magnetic resonance signal were discarded. The following pre-processing was performed using SPM functions (<http://www.fil.ion.ucl.ac.uk/spm>). As the evaluated amount of head movement within runs was less than 3 mm in translation and 2° in rotation, realignment was performed between but not within runs. Anatomical and functional images were normalised into the MNI stereotactic system of coordinates using a local template matching the contrast specificity of our images, and functional data were smoothed using an 8-mm (FWHM) isotropic Gaussian kernel. The final size of the functional voxels was set to 3 x 3 x 3 mm³.

Statistical analyses were carried out using SPM2 (<http://www.fil.ion.ucl.ac.uk/spm>). Five regressors were built up using the “HRF” basis function triggered by stimulus transitions. Each regressor modelled the event-related BOLD responses to one type of transition: Onset of an incoherent motion and its changes of direction (2D motion); apparition of a 3D object (3D onset); changes of 3D motion, 3D form or colour when a 3D object was present.

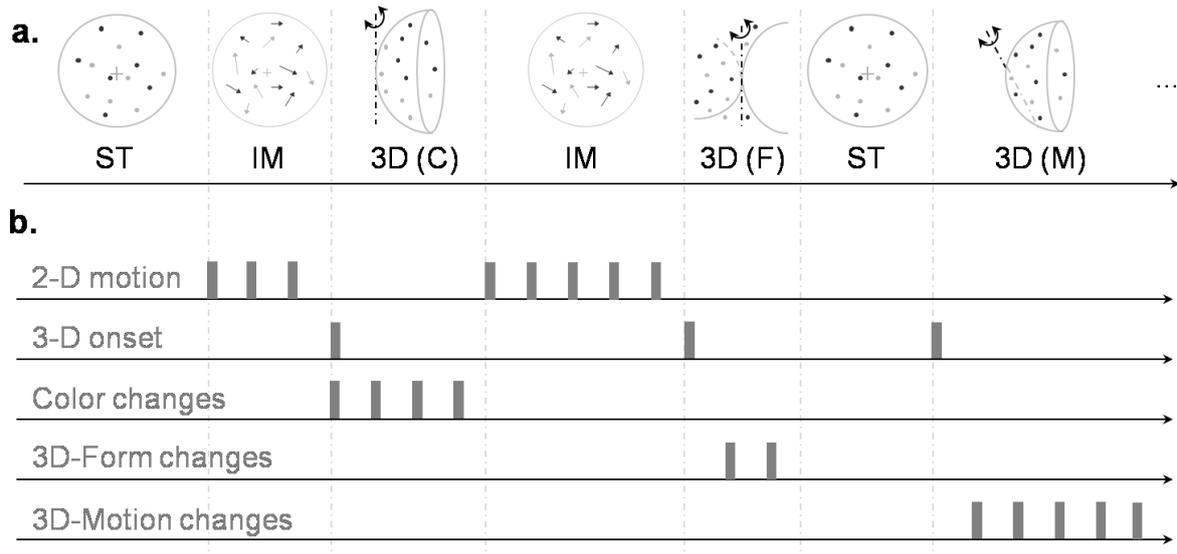
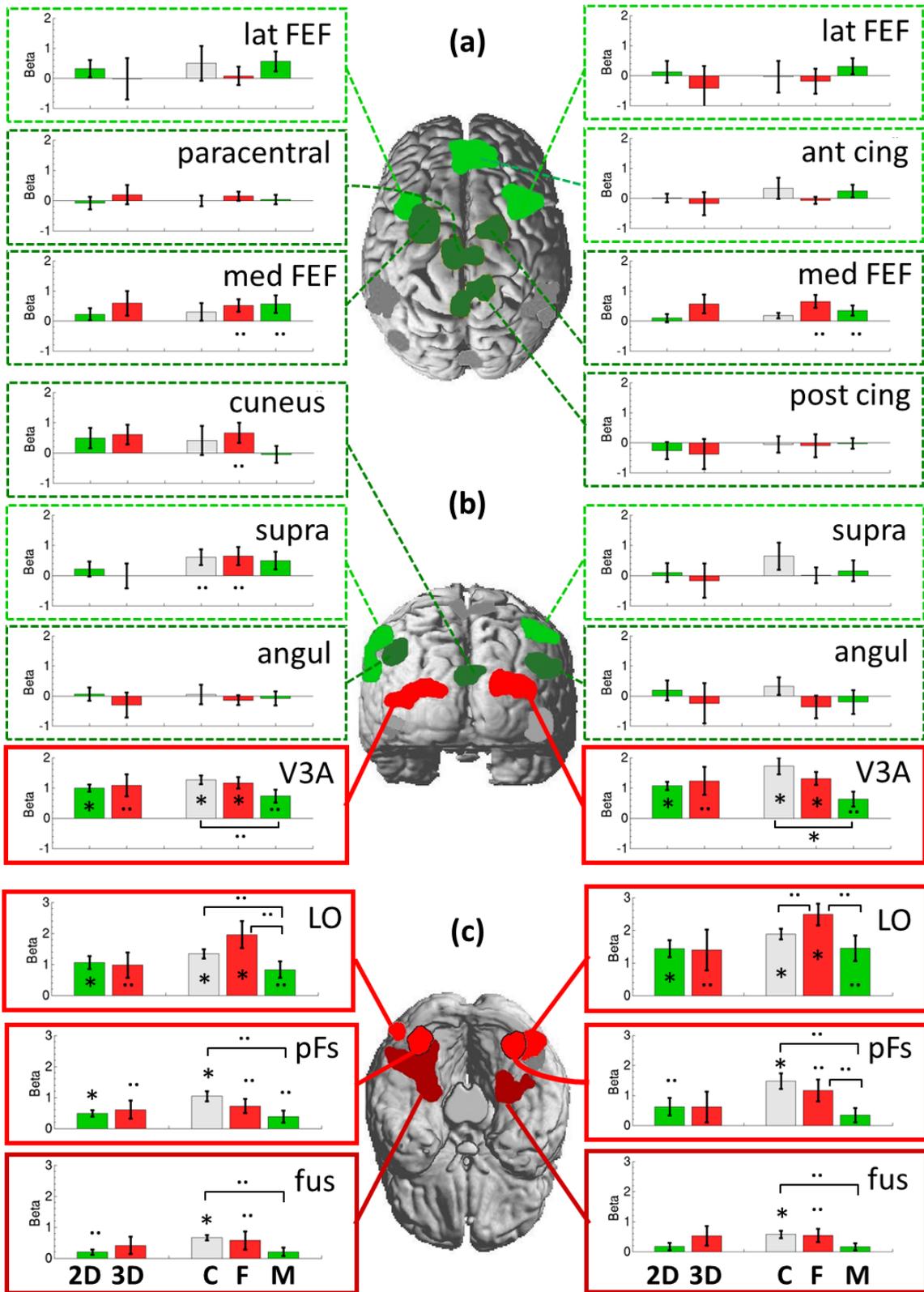


Figure 1: Experimental conditions and associated model of the BOLD response. (a) Stimulation sequence in passive viewing. The baseline consists of static dots (ST). Stimuli are either incoherent motion (IM) or three-dimensional surfaces (3D) changing colour (C), form (F) or motion direction (M) every 2s. (b) Onsets for the 5 event-related regressors modelling the fMRI signal. For the 2-D motion regressor, intervening onsets correspond to changes in local motion directions.

Individual results were entered in a second level random effect analysis, and group results were tested in selected regions of interest using the SPM toolbox MarsBaR (Brett et al., 2002; <http://marsbar.sourceforge.net/>). Activity with $p < 0.05$, corrected for multiple comparisons over the number of ROI, is considered significant.

Regions of interest (ROI)

We limited the analysis of the present passive-viewing data to areas previously found to be differentially activated for transitions of 3D form and 3D motion. Our regions of interest thus include dorsal areas that were found more activated by transitions of 3D motion and occipital and ventral areas that were more activated by form transitions. The data used to delineate these areas were acquired with the same subjects but from independent scanning runs. In these, participants underwent an active task so that form and motion transitions were either relevant or irrelevant to the on-going task (details in Paradis et al., 2008). The regions of interest are represented on Figure 2 along with their activity pattern in the passive viewing conditions. Their coordinates and spatial extent are detailed in Table 1.



Regions previously found activated for

- 3D Motion > Form ●
- Unattended transitions ●
- Form > 3D Motion ●
- Attended transitions ●
-

Figure 2: Activity profiles of the regions of interest in the passive viewing conditions (ROI). Green ROI were found more activated by 3D motion than form transitions, Red ROI were more activated by 3D form transitions. For dark ROI, the contrast between 3D motion and form was significant for attended transitions. For light ROI, the contrast between 3D attributes was significant for the transitions occurring during an incidental colour task. For each ROI, the activity profile plots the mean amplitude of response (SPM beta \pm one standard error) to each type of passively-viewed transition. From left to right: changes of motion direction in random motion (2D, green); onset of a 3D stimulus (3D, red); colour transition in the 3D stimulus (C, grey); transition of the 3D stimulus form (F, red) and transition of the 3D stimulus motion (M, green). All activity profiles are plotted using the same scale, with beta from -1 to +2 for dorsal (a) and parieto-occipital (b) areas, and beta from 0 to +3 for the ventral areas (c). Asterisks indicate responses significantly different from zero with a threshold of $p < 0.05$ corrected for the number of tested ROI. Double dots indicate responses under this threshold but with uncorrected $p < 0.05$. Areas for which no response passed the corrected threshold are bordered with dotted lines. Note that only form-related areas (red) show significant responses in passive-viewing conditions. All the responses passing the threshold in those areas had a corrected $p < 0.04$, whereas all dorsal responses had a corrected $p > 0.4$ and uncorrected $p \geq 0.02$, except in the right superior FEF where the response to the form transitions reached $p = 0.01$, uncorrected. **Abbreviations:** ant= anterior; post= posterior; lat= lateral; med= medial; cing= cingular; paracentral= paracentral lobule; FEF= frontal eye field, at the intersection of the precentral and superior frontal sulci; supra= supramarginal gyrus; angul= angular gyrus; V3A= superior-occipital sulcus; LO= lateral occipital area; pFs= posterior fusiform; fus= fusiform gyrus.

Table 1. Regions of interest (ROI)

Label	Size (mm ³)	Coordinates			Label	Size (mm ³)	Coordinates		
		x	y	z			x	y	z
Motion-selective regions					post. cing.	1728	4	-46	66
ant. cing.	2619	5	46	47	<i>POs</i>	<i>1161</i>	<i>4</i>	<i>-90</i>	<i>24</i>
lat. FEF	1215	-37	12	54	Form-selective regions				
	2403	36	14	51	SOg/IOS	2403	-31	-86	11
<i>med. FEF</i>	<i>891</i>	<i>21</i>	<i>-4</i>	<i>57</i>	(V3)	3456	30	-76	17
	<i>4344</i>	<i>-26</i>	<i>0</i>	<i>58</i>	LO	512	-44	-77	-8
<i>SMA</i>	<i>1576</i>	<i>-6</i>	<i>-19</i>	<i>61</i>		1184	49	-70	-11
IPL (supra.)	4736	-54	-46	46	pFs	976	-34	-66	-8
	3186	48	-51	49		968	36	-67	-15
<i>IPL (angul.)</i>	<i>1809</i>	<i>-48</i>	<i>-73</i>	<i>37</i>	<i>Fus</i>	<i>6291</i>	<i>-33</i>	<i>-55</i>	<i>-13</i>
	<i>736</i>	<i>48</i>	<i>-72</i>	<i>31</i>		<i>2451</i>	<i>34</i>	<i>-40</i>	<i>-16</i>

(x y z) are the coordinates of the centre of mass of the ROI in mm. Cing. = cingulate; ant. = anterior; post. = posterior; FEF = frontal eye field; lat = lateral; med = medial; SMA = supplementary motor area; IPL = inferior parietal lobule; supra.= supramarginal gyrus; angul. = angular gyrus; POs = parieto-occipital sulcus; SOg = superior occipital gyrus; IOS = intra-occipital sulcus; LO = lateral occipital; pFs = posterior fusiform; Fus = fusiform. In black, the regions that were activated by unattended transitions; in italic grey, ROI delineated by attended transitions.

RESULTS

Although of possibly small amplitude, the activity observed hereafter is always positive, that is greater than the activity during the static-dot baseline. By contrast with what was observed in the context of a task, we do not find any negative activity relative to the low level baseline.

Shape-selective ROI

All the regions of interest previously defined as selective for form transitions appear significantly activated by passively-viewed colour transitions. LO and the superior occipital areas (V3A) are significantly activated by passively-viewed changes of the 3D form (F), with maximal activation in LO, while fusiform areas (pFs and Fus) only show subthreshold activity for these (uncorrected $p = 0.01$ for pFs, uncorrected $p = 0.04$ and 0.02 for the left and right Fus). The activity related to the onset of the 3D stimulus never reaches significance (uncorrected $p = 0.01$ for both V3A; 0.02 and 0.03 for left and right LO respectively, and more than 0.03 for the fusiform areas), although it is similar in amplitude with the activity related to shape transitions in V3A.

None of the ventral ROI is significantly activated by the transitions of 3D motion (M) (uncorrected $p \leq 0.01$ for LO; ≤ 0.02 for V3A; 0.04 for left pFs and ≥ 0.05 for both fusiform and right pFs). The amplitude of activity however tightly follows that related to the random motion changes (2D), which is significant in bilateral LO, bilateral V3A and left pFs (corrected $p < 0.05$). Note that the number of 2D-motion events was about twice the number of the other events, inducing a greater statistical power.

3D-Motion-selective ROI

In contrast with the shape-selective areas, the dorsal areas do not show any significant activity related to the passively-viewed transitions with respect to the baseline (corrected $p > 0.05$). The closest-to-significance activity was found bilaterally in the dorsomedial FEF (med FEF) for the form transitions (uncorrected $p = 0.02$ and 0.01 for the left and right FEF respectively). The left supramarginal region also shows subthreshold activity for the colour and form transitions at comparable levels of significance (respectively $p = 0.02$ and $p = 0.03$, uncorrected). With similar beta values, the form-related (F) activity in PO and the 3D-motion (M) activity in both med FEF only reach $p = 0.04$, uncorrected. All other activities have uncorrected $p \geq 0.05$.

Summary

As expected, in passive viewing conditions, the ventral regions of interest are preferentially activated by colour and form transitions, and smaller activity is found in the most anterior fusiform areas which were previously delineated using attended transitions. More

surprisingly, none of the ROI is significantly activated by the 3D-motion transitions viewed passively, not even the dorsal ones which were previously selective for the 3D-motion transitions either relevant to the task or not. In addition, the dorsomedial FEF previously found selective for the attended motion transitions now reveals a tendency to respond to form transitions as well as motion transitions.

DISCUSSION

That no dorsal area be significantly activated by passively viewed transitions of the 3D stimulus seems at odds with the observation that these areas were previously activated by unattended transitions of 3D motion. To exclude artefactual causes to this discrepancy, we first examine the experimental choices and data analysis. We then discuss the possible outcome of our results.

Positive activity relative to the static baseline

Overall, we note that none of the passively viewed transitions induce decreased activity with respect to the static baseline. By contrast, decreased activity was observed in the task context. Although, we cannot exclude that this difference is due to the slightly different baselines used in the active and passive experiments, this observation is consistent with our previous suggestion that not only signal enhancement but also inhibitory mechanisms are associated with attentional selection.

Background stimulus vs. transitions

The 3D stimulus we used conveys colour, 3D-motion and form information at once. The three attributes are present and visible to the observer all the time the stimulus is displayed on the screen, which means at transitions as well as between transitions. In this study, we modelled the transitions only, assuming that the steady-state activity related to the background presence of the stimulus would be negligible related to the activity evoked by the transitions. As the activity related to the transitions is measured with respect to a static baseline, we cannot exclude that part of the activity captured at transitions be due to the background presence of the coloured 3D moving stimulus. In line with this, IOS, LO and pFs, which are the most activated areas, are part of the network usually reported to be activated by the presence of a structure-from-motion stimulus (Orban *et al.*, 1999; Paradis *et al.*, 2000; Kriegeskorte *et al.*, 2003). FEF however are also part of this network but do not appear significantly activated here. In addition, this interpretation cannot account for all the observed effects, because activity due to the background presence of the stimulus would not depend on the transition types, whereas here the amplitude of activity varies with transitions, especially between

colour and motion transitions –and particularly in right V3A, and between form and 3D-motion transitions in bilateral LO.

3D onsets: form or motion processing?

The 3D onsets were modelled separately from the 3D-motion and form transitions because the first appearance of the 3D stimulus was not supposed to enhance preferentially the process of one attribute compared to the other. May the activity profiles give us any hint that the 3D onsets may be assimilated to form or motion events?

If we except LO and the left supramarginal, it is noteworthy that the amplitude of activity related to the 3D onsets tightly follows that of the form transitions in most areas, which suggests that the onset of the 3D stimulus might rather be treated as a form event by most areas. By contrast with the form transitions however, the responses to the 3D onset never reach significance, even though there was the same number of 3D onsets compared to form transitions (15 each). As the onsets are isolated events whereas form transitions are blocked, the statistical difference might be due to the respective efficiency of these events' arrangement (Friston *et al.*, 1999).

Ventral areas

The activation of the superior occipital regions (V3A) to 2D motion and 3D form transitions viewed passively is consistent with other results (Tootell *et al.*, 1997; Paradis *et al.*, 2000; Denys, 2004) and a possible role of this area in a coarse analysis of the 3D shape, as previously suggested (Valyear *et al.*, 2006; Paradis *et al.*, 2008).

The activity in bilateral LO is maximal for the form transitions and significantly higher for this condition than for the 3D-motion transitions (Paired t-test $t > 2.01$, $p < 0.04$ in both hemispheres). These results are in line with what has been shown by Grill-Spector and colleagues (Grill-Spector *et al.*, 1998, 1999) and replicate in passive-viewing condition what was found when subject were paying attention to colour (Paradis *et al.*, 2008). They thus confirm the selectivity of LO for the form transitions independently of the task context.

Last, and consistent with our expectations, the fusiform (fus) areas that were delineated using attended transitions show the smallest amplitudes of response to the passively-viewed transitions.

Overall in the ventral pathway, the activity evoked by the unattended form and motion transitions occurring during a colour task appear as a good predictor for the activity induced by the same transitions in passive viewing. By contrast, whereas colour transitions induce

greater activity than 3D motion transitions in passive viewing, they always induced decreased activity compared to the unattended motion transitions or the static baseline during the motion task. This likely confirms that, as assumed previously, the activity observed at colour transitions in the active conditions was actually related to the task rather than the colour transition itself.

Dorsal areas

With a task context, lateral FEF showed negative or null response to unattended form and positive response to unattended motion. Although the results are below significance, the exact same tendency appears in passive viewing.

For med FEF, we had a positive or null response to unattended form transition and slightly greater response to unattended motion transitions. Here, passively-viewed form and motion transitions both induce similar subthreshold positive activity. Thus, although selective for 3D motion when this attribute is attended and competing with form in the task context, dorsomedial FEF seems sensitive to any 3D attribute transitions when there is no task. This could be consistent with medial FEF contributing to orient attention whether this is exogenously or endogenously driven: attention may be attracted by any 3D object-related event in passive-viewing, but motion transitions could be favoured compared to form in the task context because they can help update orienting information.

Similarly to Med FEF, cuneus and bilateral supramarginal areas showed subthreshold positive activity for form transitions in passive viewing. By contrast, the activity at the unattended form transitions occurring during the colour task was always negative compared to the static baseline in the three regions. The reduced activity of the cuneus in a demanding-task context is consistent with this area being part of the default mode network (Raichle *et al.*, 2001). Note that the cuneus is the only dorsal ROI revealing a possible difference between passively-viewed form transitions and 3Ds-motion transitions (uncorrected $p = 0.02$), with a greater positive response to the form transitions compared to the 3D-motion transitions.

Finally, the paracentral area, which showed maximal activity for the unattended compared to attended transitions, is among the ones showing the lowest activity whatever the transition in passive viewing.

Overall in passive viewing, the dorsal regions not only show reduced activity compared to the previous active conditions, most of them also appear to lose their selectivity for the 3D motion feature. With these results, we may wonder whether there is an automatic processing of objects' 3D motion or whether accessing this feature systematically requires attention.

Highlights

- LO is sensitive to form transitions whatever the task context.
- No “deactivation” is observed in passive viewing.
- Dorsal areas appear significantly activated by stimulus transitions in a task context only, whether the transitions are relevant to the task or not.
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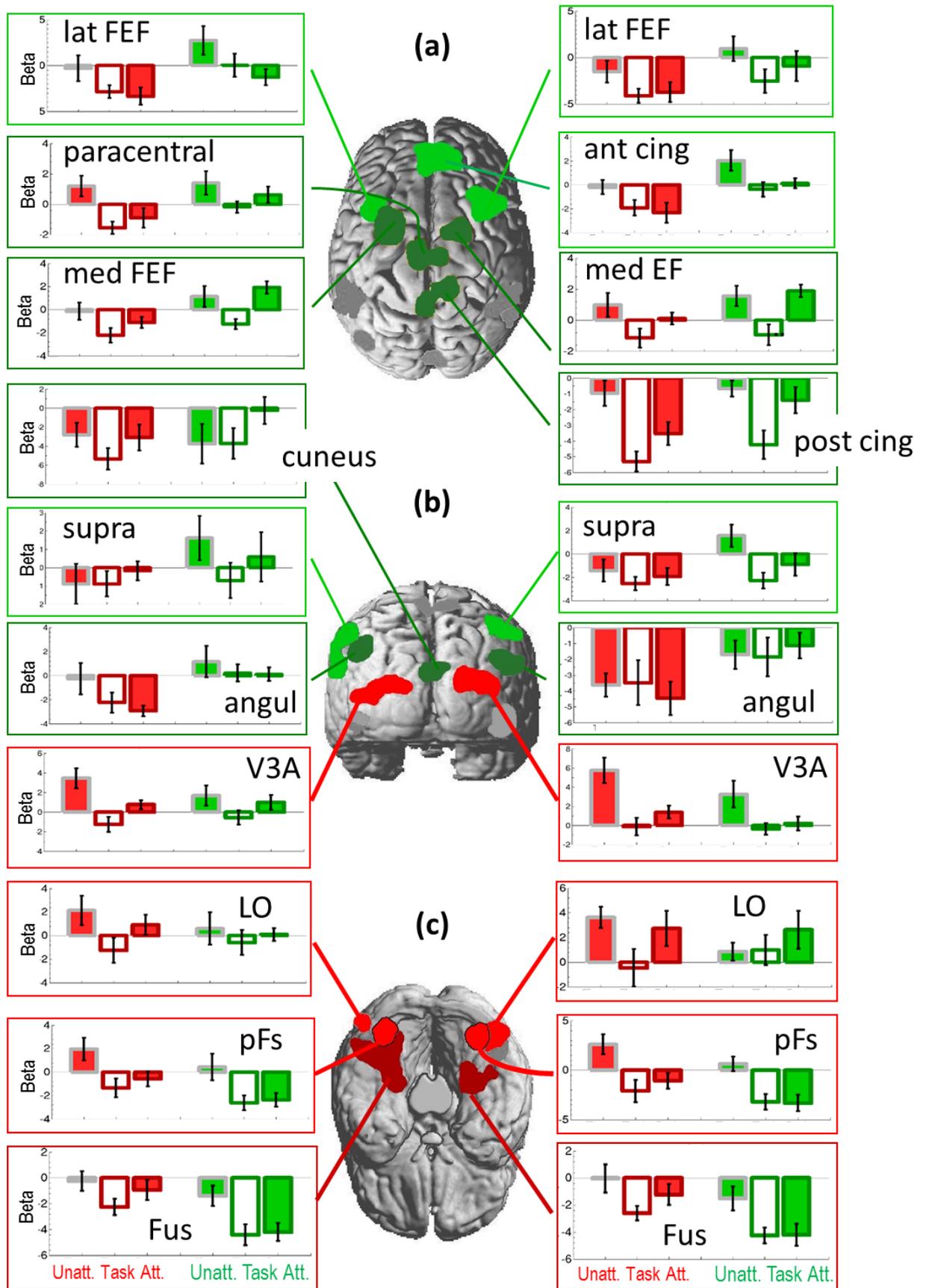
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SUPPLEMENTARY MATERIAL



Supplementary Figure 1: Activity profiles of the regions of interest in the experiment with a task context (results from Paradis *et al.*, 2008). Green ROI were found more activated by 3D motion transitions than form transitions, Red ROI were more activated form transitions. For dark ROI, the contrast between 3D motion and form was significant when the transitions were attended. For light-color ROI, the contrast between 3D attributes was significant for the unattended transitions. For each ROI, the activity profile plots the mean amplitude of response (SPM beta \pm one standard error) to each type of transition. From left to right: Unatt. = Unattended form transitions = form transitions during the incidental colour task (gray outline, red filling); Form task = colour transitions in the form task (red outline, white filling); Attended form transitions = form transitions in the form task (red outline and filling); Unattended motion transitions = motion transitions in the colour task (gray outline, green filling); Motion task = colour transitions in the motion task (green outline, white filling); Attended motion transitions = motion transitions in the motion task (green outline and filling). (a) dorsal areas, (b) parieto-occipital areas, (c) ventral areas. **Abbreviations:** ant= anterior; post= posterior; lat= lateral; med= medial; cing= cingular; paracentral= paracentral lobule; FEF= frontal eye field, at the intersection of the precentral and superior frontal sulci; supra= supramarginal gyrus; angul= angular gyrus; V3A= superior-occipital sulcus; LO= lateral occipital area; pFs= posterior fusiform; fus= fusiform gyrus.