Parallel networks operating across attentional deployment and motion processing: A multi-seed partial least squares fMRI study

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Anticipatory deployment of attention may operate through networks of
brain areas that modulate the representations of to-be-attended items
in advance of their occurrence through top-down control. Luks and
Simpson (2004) (Luks, T.L., Simpson, G.V., 2004. Preparatory deploy-
ment of attention to motion activates higher order motion-processing
brain regions. NeuroImage 22, 1515–1522) found activations in both
control areas and sensory areas during anticipatory deployment of
attention to visual motion in the absence of stimuli. In the present
follow-up analysis, we tested which network activity during anticipa-
tory deployment of attention is functionally connected with task-related
network activity during subsequent selective processing of motion
stimuli. Following a cue (anticipatory phase), participants monitored a
sequence of complex motion stimuli for a target motion pattern (task
phase). We analyzed fMR signal using a partial least squares analysis
with previously identified cue- and motion-related voxels as seed
regions. The method identified two networks that covaried with the
activity of seed regions during the cue and motion-stimulus-processing
phases of the task. We suggest that the first network, involving ventral
intraparietal sulcus, superior parietal lobule and motor areas, is related
to anticipatory and sustained visuomotor attention. Operating in
parallel to this visuomotor attention network, there is a second
network, involving visual occipital areas, frontal areas as well as
angular and supramarginal gyri, that may underlie anticipatory and
sustained visual attention processes.

Introduction

Attention is thought to modulate how sensory stimuli are
processed, via an attention network involving prefrontal, parietal
and cingulate cortical areas (Mesulam, 1981; Posner and Peterson,
1990). Attentional control is a network phenomenon in the sense
that one or more control regions drive or influence the activity in
other, task-specific regions. Prior to stimulus onset, attentional

processes may be deployed in anticipation of the oncoming stimuli
and it has been suggested that anticipatory processes might operate
by modulating stimulus representations (Desimone and Duncan,
1995). A fundamental question is how networks of areas covary in
activity between preparatory and task performance periods to
accomplish this attentional deployment and its influence on
subsequent task processing.

We examined anticipatory deployment of attention to motion in
advance of motion-stimulus presentation, and subsequent motion
processing. Several fMRI studies have provided evidence that
anticipatory deployment of attention operates by activating
internally generated representations of the to-be-attended stimulus
features (see Driver and Frackowiak, 2001, for reviews). For
example, in a visual pattern discrimination task, Kastner and
colleagues reported selectively enhanced activity in V1, V2, V4
and TEO corresponding to the location of the to-be-attended
stimulus during a preparatory phase, in the absence of visual
stimuli (Kastner et al., 1998; Kastner et al., 1999). Sensory
activations have also been reported in response to spatial and non-
spatial feature attention cues, prior to target stimulus presentation
(e.g., Corbetta et al., 2000; Giesbrecht et al., 2003; Hopfinger et al.,
2000; Macaluso et al., 2003; O'Connor et al., 2002). Two studies
have examined preparatory deployment of attention to motion
when relevant sensory stimuli were present. Chawla et al. (1999)
reported increased V5/MT+ activation while participants attended
a static dot array and prepared for a motion discrimination, relative
to preparation for a color discrimination. Shulman et al. (1999)
reported activity in V5/MT+, intraparietal sulcus (IPS) and lateral
occipital cortex while participants attended a directional arrow cue
and a randomly moving dot array in preparation for brief coherent
movement of a subset of dots in the target direction.

Luks and Simpson (2004) asked whether the anticipatory
deployment of attention modulates activity in areas that process a
to-be-attended motion-stimulus. In this fMRI study, following a
10-s cue phase without stimuli, participants monitored a sequence
of complex motion stimuli and detected a target motion pattern.
For each block of trials, one hemifield was designated as the to-be-

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attended side, where relevant stimuli would subsequently appear. If stimuli appeared in the other hemifield, participants were to ignore them. The authors identified regions that were active during the cue phase in anticipation of the motion stimuli, including higher- and lower-order motion-processing regions. They also reported lateral prefrontal and cingulate activations during the cue phase, suggesting top-down modulation of activity in task-relevant processing areas. These results support a dynamic attention network that has anticipatory-phase activity that transitions into task-processing activity when stimuli are presented.

However, it remains unclear how regions dynamically coordinate attentional deployment and task processing functions across cue and motion-processing phases of the trials. In this study, we are specifically interested in how preparatory activity during the cue period influences subsequent processing activity during the motion period. We hypothesized that attention deployment and motion-processing regions would covary in activity across the anticipatory and stimulus-processing phases of the task. Furthermore, we hypothesize that the task will involve regions that will differentially interact within multiple networks and across the preparatory and motion periods of the task. This type of dynamic progression of brain activity across task phases is not addressed by typical univariate analyses in which conditions are modeled independently. We sought a data analytic approach that would allow us to directly investigate the relationship of brain activity between anticipatory and stimulus-processing phases of a task and that would constrain our investigation to the covariance of interest—namely, the relationship between brain activity in the two task phases. To this end, we extended the seed partial least squares (PLS) multivariate analysis technique (Schreurs et al., 1997; McIntosh, 1999) to detect interactions among brain regions *between* phases of our task. We looked for brain activity during the cue and motion-processing phases that covaried with the motion-related activity of 16 seed regions: those regions that showed elevated activity during motion processing in the univariate analysis reported by Luks and Simpson (2004); and anticipatory attention-related activity of two seed regions: those that showed elevated activity during the cue phase.

We hypothesized that the PLS analysis would identify multiple networks consisting of regions whose activity covaried across cue and motion phases of the task. We also hypothesized that motion-processing seed activity would correlate with preparatory network activity during the cue period, supporting the influence of preparatory activity in an interactive network on subsequent motion processing in specific brain regions. We further hypothesized that cue-period seed activity would correlate with motion-processing-related network activity during the motion-processing period, supporting the influence of preparatory activity in those seed regions on subsequent motion processing. These relationships between the activity of more general processing networks and specific regions in specific phases of the task allow us to examine mixtures of processes at play (e.g., visual attentional deployment, motor preparation, and motion target detection).

The method allows us to detect activity that was correlated both within and between conditions. However, our specific hypotheses regarded the between-condition correlations. First, if the cue-related activity of the two left ventral intraparietal sulcus seed regions reflects preparatory attention processes that aid in mobilizing a subsequent motion-stimulus-processing network, then those seeds should correlate reliably with motion-stimulus-processing region during stimulus presentation. If this hypoth-

esis is wrong, then correlations between preparatory-phase seeds and activity during the motion-stimulus-processing condition should be non-significant or, conceivably, significant but for areas unrelated to the task (e.g., a self-monitoring interpretation). Second, we reasoned that the prior univariate analyses may have identified preparatory activity that exhibited significant changes from baseline on average, but there could be other preparatory areas whose mean activation levels were zero but whose variability around this zero mean nonetheless influenced the subsequent activation of a motion-processing network. Put differently, some subjects may activate certain regions and others may deactivate them, but the advantage for mobilizing the motion-processing network may depend on activating those preparatory regions. We thus hypothesized that the correlations between motion-processing seeds and activity during the preparatory period would reveal additional preparatory activity in regions that reflect variability in subject-specific processes.

Methods

The data presented here were previously analyzed by Luks and Simpson (2004). Thus, the experimental methods are identical, and are summarized here.

Participants

Twelve participants (4 women, 8 men) volunteered for cash compensation. All were right-handed, neurologically normal, aged 20–40, with graduate or post-graduate education levels and normal or corrected-to-normal vision.

Cued visual motion task

Materials

The stimuli used for motion identification consisted of a circular patch (diameter = 6°) of randomly arranged white dots (diameter = 15°, density = 0.8 dots/degree) moving coherently with variable rotation (left, right or no rotation) and dilation (expansion, contraction or no dilation). Movement was created by displaying 6 images for 50 ms with 10 ms between images. Motion stimuli were presented in the lower left or lower right quadrant of the screen, with a fixation cross in the center. Each motion-stimulus was presented for 350 ms, with an inter-stimulus interval of 650 ms. The fixation stimulus was a small cross. The cue stimulus was a slight enlargement of the fixation stimulus.

Stimulus presentation was controlled with Psyscope 1.25 on a Macintosh PowerPC computer. Participants' responses and scanner pulses were recorded. Stimuli were back-projected onto a screen at the participants' feet and viewed through a mirror mounted on the head coil. Participants made finger-press responses on a fiber-optic button 8-channel response pad (Lightwave Medical Industries Ltd., Vancouver BC). The response pad also collected scanner TTL pulses generated at the onset of each image acquisition. Scanner signals were input to a Psyscope button box and recorded by the Psyscope presentation program. The Psyscope software generated a data file containing recorded event times for all stimulus presentation events, responses and scanner TTL pulses, allowing for precise retrospective temporal synchronization of stimulus events and image acquisition.

Procedure

The experiment consisted of 10 blocks of 6 trials each. Prior to each block, participants were instructed to attend to either the left or right visual field for the entire block (the attended side was counterbalanced within each session) and an example of a target motion-stimulus (e.g., right rotating and expanding) was presented.

Each trial began with a 10 s fixation period ("BASELINE" phase) followed by a 250 ms enlargement of the fixation marker which cued participants to prepare for the motion stimuli in the attended visual field. The cue was followed by a 9.75 s fixation period ("CUE" phase), except on 1/5 of the trials, in which the fixation period lasted only 1.25 s. These short trials served as catch trials, to motivate participants to begin preparing for the motion stimuli immediately after the cue, despite there being a long interval between cue and motion stimuli on most trials. Cue-specific preparatory sensory activity has been previously reported using these cue period durations (Hopfinger et al., 2000; Kastrup et al., 1998; Kastner et al., 1999) and catch trials (Hopfinger et al., 2000). We excluded these catch trials from the partial least squares analysis. Next, a sequence of 10 motion stimuli was presented for 10 s ("MOTION" phase). The target pattern occurred 1–3 times within a block of motion stimuli. On 50% of trials, the motion stimuli appeared in the attended visual field, in which case participants monitored the stimuli for the target and made a button-press response; in the other 50% of trials, motion stimuli appeared in the unattended visual field, and participants ignored them. The unattended phase was not included in the present analyses.

Functional MRI acquisition

Blood oxygenation level dependent (BOLD) fMRI activity (Kwong et al., 1992; Ogawa et al., 1990) was recorded with a 1.5 T GE Signa LX 8.3 scanner (Milwaukee, WI) using a gradient-recalled echo-planar (EPI) sequence (TR = 3 s, TE = 50 ms, flip angle = 60°, matrix = 128 × 128 voxels, field of view = 26 × 26 cm, 19 slices, thickness = 5 mm, gap = 1 mm). Anatomical images were acquired with a high-resolution T1-weighted rf-spoiled GRASS sequence.

Cross-condition multi-seed partial least squares analysis

Each trial was broken up into the BASELINE periods (fixation intervals used as baselines) and two experimental conditions: (i) CUE phase, between the enlargement of the fixation and the onset of the first stimuli; this involved fixation behavior but presumably invoked preparatory attention processes as well, (ii) MOTION phase, comprising those blocks of 10 motion stimuli that were presented in the attended hemifield.

Previous analysis identified regions that showed elevated activity during CUE and MOTION with respect to BASELINE (Luks and Simpson, 2004). In that previous analysis, data were submitted to a mixed-design GLM analysis, fitting a reference hemodynamic response function (HRF) to the observed time series data. Fixation and motion stimuli conditions were modeled as epochs convolved with the HRF (Fixation = 10-s epoch, Motion = 11-s epoch) and cues were modeled as events. Contrasts of interest were performed on individual subject data. Second-level one sample t tests were performed on the combined individual results to create random-effect group analyses for each contrast (n = 12). Peak locations within each activation cluster in visual processing regions from the

MOTION > BASELINE and CUE > BASELINE contrasts were used as "seed" voxels in the present PLS analysis.

That univariate analysis gave us a set of regions with increased or reduced activity in each condition. It does not tell us how brain activity relates *among* the regions, nor how it relates between the two conditions. Within a condition, one can estimate functional connectivity by asking whether sets of regions vary their activity together across participants. If they do, that would suggest that they comprise an interactive network. If instead, the brain regions vary their activity independently of each other across participants, that would suggest that they are simply activated (or deactivated) at the same times, but not as part of a larger network. This is the approach taken in seed PLS (Della-Maggiore et al., 2000; McIntosh, 1999). However, we can take this approach further by analyzing the relationship between activity of brain regions from one condition and activity in another condition. In this study, we are interested in brain activity during CUE and brain activity during MOTION conditions that covary across participants. If activity is independent between the two conditions, that would suggest that CUE-related activity and MOTION-related activity occur in distinct, unrelated stages. If, however, the activity of some regions during the CUE phase covaried with the later activity of MOTION-related seed regions, that would suggest that brain activity in the two conditions is related. In this case, anticipatory CUE activity may influence subsequent motion-stimulus-processing activity. Likewise, if activity of some regions during the MOTION condition covaried with previous activity of the CUE-related seed regions, that would suggest that the heightened activity of seed regions during CUE influences the activity of regions during subsequent motion-stimulus processing.

To this end, we adapted the seed region PLS method (Della-Maggiore et al., 2000; McIntosh, 1999). PLS is a multivariate technique that describes the relationship between a set of two or more blocks of data, in our case, seed region activity in each task condition and activity in other regions (McIntosh et al., 1996; McIntosh et al., 1998; Schreurs et al., 1997). In the case of cross-condition multi-seed PLS (depicted in Fig. 1), we analyze how brain activity in the two conditions covaries with the activity of multiple seed voxels. The seed voxels used, listed in Table 1, are selected based on prior functional analysis. If a seed region showed a significant change in activity (compared to BASELINE) during the CUE condition, then we focus on its activity during CUE; if it showed changed activity during the MOTION condition, then we focus on its activity during MOTION. Next, we compute the correlation between each seed voxel during its respective condition (CUE or MOTION) with the activity of each voxel in the brain separately during CUE and MOTION conditions, resulting in two correlation maps per seed region. The correlation is computed across participants.

The voxel values (including seed voxels) are averaged over a 4-TR window/12 s duration,[1] relative to reference scans in order to remove baseline drift across the testing session. The reference was chosen to be the third TR within the BASELINE period. The third TR was chosen because participants were aware of the long, 10-s BASELINE. Thus, activity early on during

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[1] We initially applied spatiotemporal version of this PLS analysis (McIntosh et al., 2004) to search for potential changes over successive TRs within the CUE and MOTION blocks. However, the spatiotemporal analysis resulted in relatively stable time courses. Without loss of specificity, we therefore reverted to the simpler, block-design PLS analysis presented here.
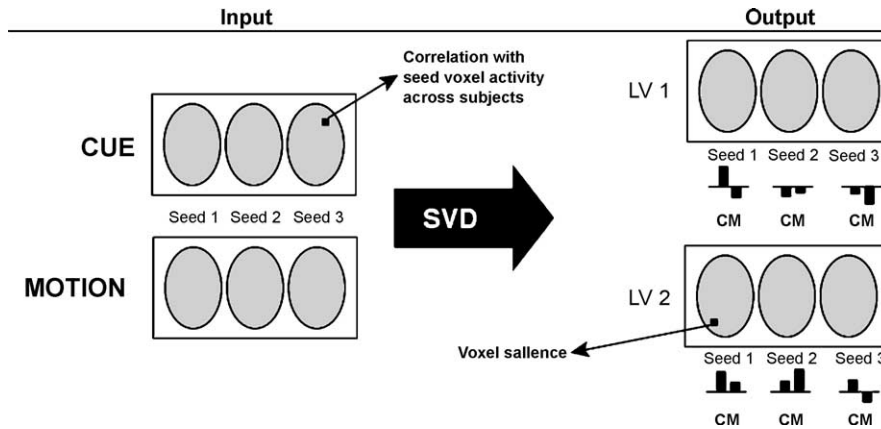
Fig. 1. Schematic of the cross-condition multi-seed PLS analysis. Input: a matrix containing the correlation between each voxel's activity and the seed voxel activity (during the seed condition) across participants, as a function of condition. SVD: a singular value decomposition breaks down the input matrix into latent variables (LVs) that best account for the correlation structure. Output: the brain maps plot the "brain LV," showing the networks of brain activity that differ across task conditions in terms of the correlation with the seed voxel's seed/condition activity (computed across participants). The bar graphs plot the "seed saliences," indicating the extent to which the LV explains the correlation between the brain LV network and seed-voxel activity in each condition.

BASELINE is expected to be more unpredictable and serve as a less stable baseline than activity near the end of BASELINE. Note that the same baseline applied to both CUE and MOTION conditions for each trial.

PLS uses a singular value decomposition (SVD) applied to compute an optimal least-squares fit to a matrix that relates the input (in our case, the seed region activity as a function of task conditions) to the measured output variables (in our case, the activity of other regions in the brain). This matrix is constructed from two matrices, **M** and **A**. **M** is the data matrix and is constructed by placing task conditions in rows and voxels in columns and thus has dimensions $n_k n_o \times n_v$ where n_k is the number of conditions (2 in our case), n_o is the number of observations (i.e., number of subjects) and n_v is the number of voxels. **A** contains the voxel activity for the n_l seeds (here $n_1 = 18$), with one seed per column. Each seed is taken from its respective condition, either CUE or MOTION. For each condition k, $\mathbf{R}_k$ is a submatrix containing the correlations between seed activity and voxel activity:

$$\mathbf{R}_k = \mathbf{A}^T * \mathbf{M}_k / (n_k - l).$$

Note that unlike previous seed PLS methods, each seed is correlated with voxel activity from each condition. These $\mathbf{R}_k$ matrices are stacked columnwise into one large matrix **R** and subjected to SVD.

$$[\mathbf{USV}] = SVD[\mathbf{R}^T]$$

where **U** is a $n_v \times n_k n_l$ orthonormal matrix containing voxel saliences, **V** is a $n_k n_l \times n_k n_l$ orthonormal matrix of seed/condition saliences and **S** is a diagonal matrix of the $n_k n_l$ singular values. Pairs of column vectors from **U** and **V**; $\mathbf{u}_j$ and $\mathbf{v}_j$, respectively, comprise latent variables (LVs) where $\mathbf{u}_j$ is the singular image ("brain LV," or the brain portion of the latent variable) and $\mathbf{v}_j$ is the singular profile ("seed LV," or the seed portion of the latent variable), and these are connected by the singular value s_j which is the square root of the eigenvalue. The singular value indicates how much of the covariance of the input matrix is accounted for by its respective LV. Brain LVs consist of a vector of voxel saliences whose strength covaries with each seed's activity across partic-

ipants. The numerical weights within the brain LV are called "saliences" and can be positive or negative, indicating the degree to which each voxel is related to the design contrast. The seed LV reveals the nature of the brain-seed covariance, and in particular, how this covariance varies across task conditions (it is analogous to a contrast).

The significance of each LV is assessed with a permutation test (500 iterations) in which task condition labels are shuffled. This results in a distribution of singular values from shuffled data sets, from which the cumulative 95th percentile is taken as the significance threshold. The reliability of each voxel's contribution to the LV is assessed by a bootstrap estimation of standard errors for the voxel salience (100 iterations) by resampling participants. Each voxel salience can be expressed as a bootstrap ratio, or the probability that each voxel salience is non-zero. Thus, the bootstrap assessment of voxel saliences evaluates how stable the brain LV maps are across participants. We also use the results of the bootstrap to similarly compute standard errors on seed-brain LV correlations to identify task conditions for each seed that has a reliably non-zero seed activity–brain activity relationship.

Finally, cluster analyses were used to identify significant regions involved in the LVs. Clusters were considered significant if 15 contiguous voxels exhibited a single-voxel bootstrap ratio of 3.3 (roughly equivalent to a z score with probability 0.001).

Results

We hypothesized that the PLS would identify multiple networks consisting of regions whose activity covaried across cue and motion phases of the task. We also hypothesized that MOTION seed activity would correlate with preparatory network activity during the cue period, supporting the influence of preparatory activity in an interactive network on subsequent motion processing in specific brain regions. We further hypothesized that CUE seed activity would correlate with motion-processing-related network activity during the MOTION period, supporting the influence of preparatory activity in those seed regions on subsequent motion processing.

Table 1
Seed voxels used in the cross-condition seed PLS analysis

Seed #	Region	MNI[a] coordinates	Seed condition[b]
MOTION			
1	R angular gyrus and supramarginal gyrus	(42, −56, 3)	MOTION
2	L ventral intraparietal sulcus	(−34, −58, 36)	MOTION
3	L V5/MT+	(−38, −66, −10)	MOTION
4	R ventral intraparietal sulcus	(36, −50, 32)	MOTION
5	R angular gyrus and supramarginal gyrus	(32, −64, 28)	MOTION
6	L V3	(−26, −80, 8)	MOTION
7	R ventral intraparietal sulcus	(24, −76, 28)	MOTION
8	R ventral intraparietal sulcus	(24, −76, 36)	MOTION
9	L posterior insular cortex	(56, −40, 28)	MOTION
10	L angular gyrus and supramarginal gyrus	(−46, −52, 56)	MOTION
11	L V3	(−26, −84, 8)	MOTION
12	R angular gyrus and supramarginal gyrus	(34, −50, 26)	MOTION
13	R angular gyrus and supramarginal gyrus	(38, −68, 50)	MOTION
14	L V5/MT+	(−42, −68, −14)	MOTION
15	L ventral intraparietal sulcus	(−32, −74, 44)	MOTION
16	R angular gyrus and supramarginal gyrus	(46, −48, 34)	MOTION
CUE			
17	L ventral intraparietal sulcus	(−30, −62, 42)	CUE
18	L ventral intraparietal sulcus	(−26, −76, 50)	CUE

[a] Montreal Neurological Institute coordinates (x, y, z) mm.
[b] Condition from which the seed activity was taken (the condition in which this voxel showed significant activation relative to fixation in prior analysis). The first 16 seeds were taken from the MOTION condition; the last two seeds were taken from the CUE condition.

The cross-condition multi-seed PLS yielded two significant latent variables (LVs; $P < 0.05$ by permutation test). Each latent variable reflects a network of regions whose activity covaried across the cue and motion phases of the task. Here, we report and describe the two LVs, including how each of the identified activity networks relates to each of the seed voxels' activity during each condition.

LV 1

The first latent variable (LV1) identified a network of regions whose activity covaries across task conditions. LV1 accounted for 16.8% of the cross-block covariance. The network (brain LV1) is plotted in Fig. 2 and the significant clusters are listed in Table 2.
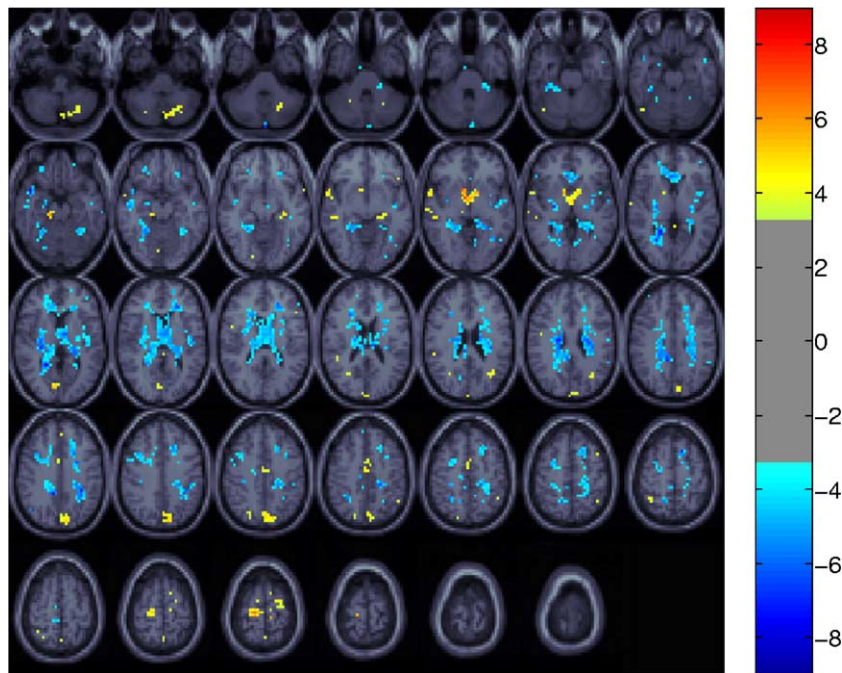

Fig. 2. The LV1 network (brain LV bootstrap ratios, plotting only significant clusters) for the first LV identified by multi-seed PLS analysis. These axial views are arranged from inferior ($MNI_z = 0.52$ mm) to superior ($MNI_z = +80$ mm) moving from left to right and top to bottom. The color scale denotes the bootstrap ratio.

Table 2
The clusters identified in the brain LV1 produced by the multi-seed PLS

LV1 cluster	Region	x	y	z	Voxels[a]	Bootstrap
Positive salience						
1	L basal ganglia	−8	−4	−8	45	7.3
2	L precentral gyrus	−16	−24	68	23	6.8
3	R cuneus	8	−84	32	46	5.0
4	R posterior cerebellum	8	−76	−48	31	4.9
Negative salience						
5	R ventral inferior parietal sulcus/superior parietal lobe	32	−40	32	1111	8.3
6	L/R basal ganglia	44	−20	8	23	4.9
7	White matter/ventricles	−40	12	36	49	4.8
8	White matter/ventricles	−28	0	52	22	4.7
9	R lateral/medial cerebellum	28	−52	−24	17	4.5

(x, y, z) coordinates are in mm according to the MNI standard.

[a] Voxels refers to the number of voxels in the cluster. 'Bootstrap' refers to the bootstrap ratio which indicates robustness across participants. Clusters 7 and 8 may be artifactual (see main text).

The regions involved in the LV1 network (Table 2) with negative saliences (those contributing greater activity during CUE and less during MOTION) included right superior parietal lobule and right ventral intraparietal sulcus, bilateral basal ganglia, two clusters in left middle frontal gyrus and right anterior cerebellum. While there may be relevant activity in frontal cortex and basal ganglia during the anticipatory phase, the extension of this cluster into white matter and ventricles is a cause for caution in interpreting this cluster as non-artifactual (clusters 7 and 8 in Table 2).
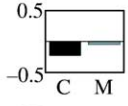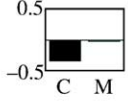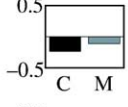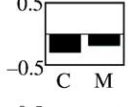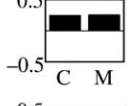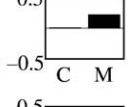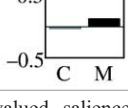
The regions with positive saliences (those contributing greater activity during MOTION than CUE) included left precentral gyrus, right cuneus, right posterior cerebellum and left basal ganglia.

This network heavily involves areas implicated in visuospatial attention and associations between visual stimuli and motor responses, and the motor responses themselves (intraparietal sulcus, superior parietal lobule, motor cortex, basal ganglia and thalamus).

To further understand how this dynamic attention network interacts with motion-processing regions, we examined the correlation between the network's activity in the CUE and MOTION phases, and the seed regions' activity at the time of MOTION processing (showing significant activity in prior univariate analysis) for seed regions 1–16 and seed regions' activity at the time of CUE for seed regions 17 and 18. These are plotted in Table 3 for seed regions with reliable contributions to the latent variable as assessed by the bootstrap.

This portion of the PLS results show us how the activity in the LV1 network relates to each of the seed voxels' activity during each condition (via the "seed salience"). Certain patterns of seed saliences could help us identify brain activity related to anticipatory processes that influence later motion processing. The bar graphs in the third column of Table 3 reflect this relationship between the activity of the LV1 network as a whole during the CUE phase (C salience) or MOTION phase (M salience) and the activity of the seed region during the MOTION phase (MOTION seeds) or CUE phase (CUE seeds). For example, a positive C salience for a MOTION seed indicates that the positive regions of LV1 (those in red hues in Fig. 2) have increased activity during the CUE phase when the seed region has

Table 3
Seed voxels reliably (according to the bootstrap test) contributing to LV1 (see Table 1 for more details on the seeds)

Seed #	(Region)	Seed–Condition Saliences (LV 1)[1]
MOTION		
1	(Angular Gyr. & Supramarginal Gyr.)	
2	(L Ventral Intraparietal Sulc.)	
3	(L V5/MT+)	
4	(R Ventral Intraparietal Sulc.)	
5	(R Angular Gyr. & Supramarginal Gyr.)	
6	(L V3)	
10	(L Angular Gyr. & Supramarginal Gyr.)	

[1] Task profiles for each seed from LV1. A large-valued salience in condition CUE (C) or MOTION (M) reflects a strong seed–brain LV1 correlation during that condition. Black bars reflect significant correlations by bootstrap (95% confidence intervals non-overlapping with zero correlation); grey bars failed to reach significance. Note that only seed voxels taken from the MOTION condition contributed reliably to this particular LV.

subsequently increased activity during the MOTION phase. Conversely, negative regions of the LV1 (those in blue hues in Fig. 2) have lowered activity during the CUE phase when the seed region subsequently has increased activity during the MOTION phase. Alternatively, a negative C salience for a MOTION indicates that the positive regions (red) of LV1 have reduced activity during the CUE phase when the seed region subsequently has increased activity during the MOTION phase, and negative regions of LV1 have increased activity during the CUE phase when the seed region subsequently has increased activity during the MOTION phase. The same logic applies to the interpretation of the M saliences (e.g., M values in the third column of Table 3). For example, a negative M salience for a MOTION seed indicates that the positive regions of LV1 (red) have reduced activity during the MOTION phase when the seed region has increased activity during the MOTION phase.

We observed three different patterns of activity in these relationships: seed regions whose activity was significantly correlated with the activity of the network MOTION but not during CUE, seed regions whose activity was significantly correlated with the activity of the network during CUE but not MOTION and seed regions whose activity was significantly correlated with the network during both phases.

Significant MOTION phase correlations

Activity in left angular gyrus/supramarginal gyrus and left V3 during MOTION was increased when activity in the LV1 network during MOTION period was increased. These correlations do not cross between conditions. Thus, these seed regions may underlie aspects of motion-stimulus processing that do not benefit directly from prior activation of the LV1 network during CUE. Activity in these regions may reflect integration of motion-stimulus processing with response preparation and selection.

Significant CUE phase correlations

Activity in right angular gyrus/supramarginal gyrus, left ventral intraparietal sulcus and left V5/MT+ was *decreased* during MOTION stimuli when activity in the LV1 network during the CUE phase was increased. But this reflects a *positive* correlation between the regions in the LV1 network that were activated during CUE (negative saliences in Table 3). Thus, the activity of these areas during motion processing may be benefiting directly from the anticipatory motor or visuospatial processing network that was previously activated during CUE.

Significant CUE and MOTION phase correlations

Activity in right angular gyrus/supramarginal gyrus during motion stimuli is increased when the network is more active in both CUE and MOTION phases. Correlation with the LV1 network in both conditions suggests that these motion-processing regions were activated in preparation for motion stimuli, and that this activity was sustained through the anticipatory phase and throughout motion-stimulus processing.

Interestingly, right ventral intraparietal sulcus was negatively correlated with activity of this network's activity during both CUE and MOTION. Thus, the decreases in right ventral intraparietal sulcus activity throughout the trial are associated with greater network activity during both anticipatory and motion-processing phases of the task.

LV 2

The second latent variable (LV2) identified a second network of regions whose activity covaries across task conditions. LV2 accounted for 13.0% of the cross-block covariance. The network (brain LV2) is plotted in Fig. 3 and the significant clusters are listed in Table 4.
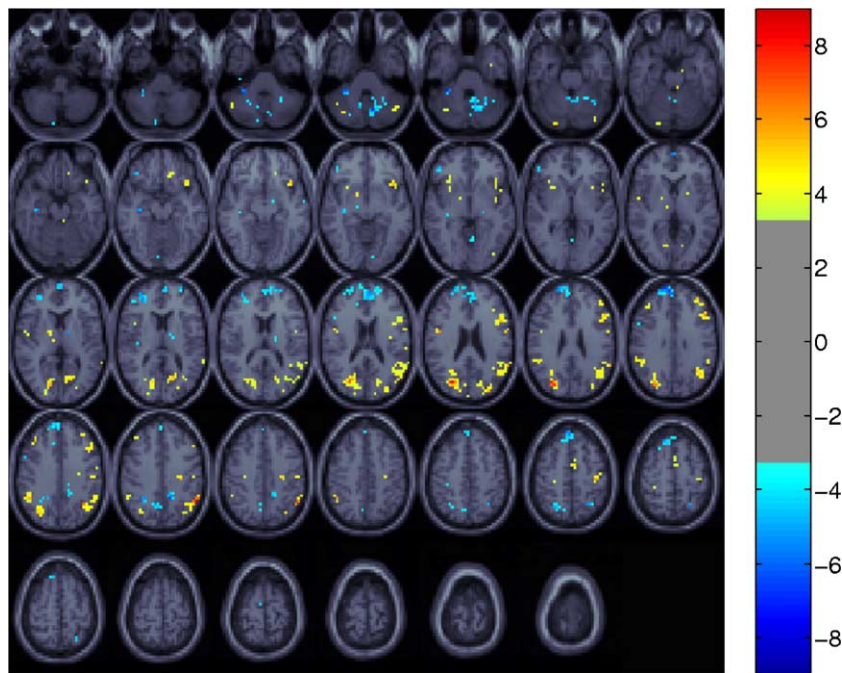

Fig. 3. The LV2 network (brain LV bootstrap ratios, plotting only significant clusters) for the second LV identified by multi-seed PLS analysis. These axial views are arranged from inferior ($MNI_z = 0.52$ mm) to superior ($MNI_z = +80$ mm) moving from left to right and top to bottom. The color scale denotes the bootstrap ratio.

Table 4
The clusters identified in brain LV2 produced by the multi-seed PLS

LV2 cluster	Region	x	y	z	Voxels[a]	Bootstrap
Positive salience						
1	L medial occipital gyrus	−28	−76	20	100	8.6
2	L/R angular gyrus and supramarginal gyrus	52	−56	36	92	8.4
3	R middle frontal gyrus	48	20	28	38	6.2
4	L/R lateral occipital/temporal	−48	−52	32	27	5.6
5	R inferior frontal gyrus	40	16	−12	17	5.4
6	R cuneus	12	−72	4	28	5.3
Negative salience						
7	L superior/medial prefrontal gyrus	−8	56	28	96	6.8
8	R posterior cerebellum	8	−68	−40	36	6.6
9	L superior/medial prefrontal gyrus	−4	40	52	25	5.8
10	L middle frontal gyrus	−32	44	8	19	5.2

(x, y, z) coordinates are in mm according to the MNI standard.

[a] Voxels refers to the number of voxels in the cluster. 'Bootstrap' refers to the bootstrap ratio which indicates robustness across participants.

The regions with negative saliences (more active during the anticipatory phase and less active during attended motion) include left lateral and bilateral medial prefrontal regions. The regions with positive saliences (more active during motion processing than the anticipatory phase) were right prefrontal regions and higher-level visual motion processing and visuospatial attention areas (left medial occipital gyrus, ventral intraparietal sulcus, angular gyrus/ supramarginal gyrus).

To further understand how this dynamic attention network interacts with motion-processing regions, we examined the correlation between the network's activity in the CUE and MOTION phases, and the seed region activity during MOTION (showing significant activity in prior univariate analysis) for MOTION seed regions, and during the CUE phase for CUE seed regions. These are plotted in Table 5 for seed regions with reliable contributions to the latent variable as assessed by the bootstrap. We observed three different patterns of activity in these relationships: seed regions whose activity was significantly correlated with the activity of the network during MOTION but not during CUE, seed regions whose activity was significantly correlated with the activity of the network during CUE but not MOTION and seed regions whose activity was significantly correlated with the network during both phases.

Significant MOTION phase correlations

Activity in right posterior insular cortex, left angular gyrus/ supramarginal gyrus and left V3 during MOTION was increased when activity in the LV2 network during MOTION was elevated. These correlations do not cross between conditions. Thus, these seed regions may underlie aspects of motion-stimulus processing that do not benefit directly from prior activation of the LV2 network during CUE. These areas may coordinate with the positive regions in the LV2 network to carry out motion-stimulus processing.

Significant CUE phase correlations

Areas in right angular gyrus/supramarginal gyrus, right ventral intraparietal sulcus and left V3 were more active during MOTION when the LV2 network was previously more active during CUE. These could represent areas that have greater activity as a result of greater prior biasing by the brain LV2 areas.

Significant CUE and MOTION phase correlations with CUE seeds

Activity during CUE of one left ventral intraparietal sulcus seed (#18) correlated positively with the LV2 network's activity during both phases. For the other left ventral intraparietal sulcus seed (#17), its CUE activity correlated negatively with subsequent activity of the LV2 network during MOTION, and while non-significant, also with the LV2 network's activity during CUE. These two regions thus may reflect visuospatial attention activity that initiates during the CUE and is sustained during MOTION to improve the efficacy of motion-stimulus processing or responding.
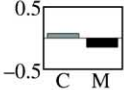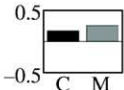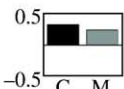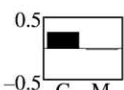
Discussion
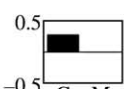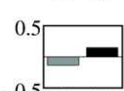
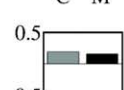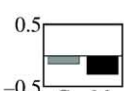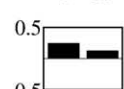We examined how network activity evolves from the anticipatory attention deployment phase to the subsequent motion-stimulus-processing phase. Standard univariate approaches do not lend themselves to this type of analysis. To this end, we extended prior seed PLS methods to identify activity that covaried between the two task conditions. We seeded with regions that previously showed elevated activity (relative to fixation) in the CUE (anticipatory attention) or MOTION (motion-stimulus processing) phases. This method enabled us to find two different cortical networks operating in parallel. The study examined anticipatory deployment of visual attention followed by sustained visual processing of motion and motor attention. While the experiment was aimed at visual attention, it implicitly included a strong motor attention component. The cortical constituents of the two networks revealed by our method are consistent with visual attention (Corbetta and Shulman, 1998; Hopfinger et al., 2000) and motor attention regions (Rushworth et al., 2001; Rushworth et al., 2003). However, they do not differentiate strictly along those lines, and may reveal a mixture of motor and visual attention systems, consistent with the task. The relationships between activations across phases of the task were not evident in prior analyses (Luks and Simpson, 2004).

Two attention networks

In particular, the cross-condition seed region PLS identified two attention networks that involve different subsets of regions

Table 5
Seed voxels reliably (by bootstrap) contributing to LV2 (Table 1 for seed information)

Seed #	(Region)	Seed–Condition Saliences (LV 2)[1]
MOTION		
2	(L Ventral Intraparietal Sulc.)	
5	(R Angular Gyr. & Supramarginal Gyr.)	
6	(L V3)	
7	(R Ventral Intraparietal Sulc.)	
8	(R Ventral Intraparietal Sulc.)	
9	(L Posterior Insular Cortex)	
10	(L Angular Gyr. & Supramarginal Gyr.)	
11	(L V3)	
CUE		
17	(L Ventral Intraparietal Sulc.)	
18	(L Ventral Intraparietal Sulc.)	

[1] Task profiles for each seed from LV2. A large-valued salience in condition CUE (C) and MOTION (M) reflects a strong seed–brain LV2 correlation. Black bars plot significant correlations by bootstrap (95% confidence intervals non-overlapping with zero correlation); grey bars failed to reach significance. The last two seeds were taken from the CUE condition; the remaining seeds were taken from MOTION.

commonly found in attention studies. Based on previous literature investigating the functions of these regions in isolation, we hypothesize that these networks subserve two different functions involved in deployment of attention over task phases: integration of attention to response selection and action with visual processing ("visuomotor attention," LV1) and attention to visuospatial motion processing ("visual attention," LV2). The seed–LV relationships reveal different areas that have correlated activity with these dynamic networks during the cue or motion-processing phases, or both. These relationships reveal how the attention networks may activate or recruit more specific stimulus-processing regions during anticipatory and target processing phases.

A visuomotor attention network

The network identified in LV1 includes regions frequently implicated in motor preparation, visuomotor integration and motor activity. It may reflect a primarily visuomotor-attention network, consisting of regions involved in motor selection and performance (motor cortex), motor preparation and inhibition (basal ganglia) and motor attention (dorsal medial intraparietal sulcus, superior parietal lobule and supramarginal gyrus), as proposed by Rushworth et al. (2001, 2003). Rushworth and colleagues suggested that human parietal cortex, like primate parietal cortex, is organized with complementary regional specializations for orienting attention. One specialization is in the visuospatial modality and another is in the motor-spatial modality. Areas implicated in covertly shifting attention in visual space are closely linked with areas involved in overt eye movements, and include intraparietal sulcus on the lateral/ventral bank of the sulcus, and adjacent parietal–occipital junction and angular gyrus. Rushworth et al. (2001) found that transcranial magnetic stimulation of left ventral intraparietal sulcus (but not the right) disrupted shifting of motor attention. Rushworth et al. (2001, 2003) thus proposed that the medial/dorsal bank of IPS, adjacent superior parietal lobule (SPL) and supramarginal gyrus areas subserve a similar function of covertly shifting attention to motor space/behavior that is linked to the planning of overt reorienting of motor behavior (limb or finger movements). Consistent with this reasoning, Johnson et al. (2002) found intraparietal sulcus and superior parietal lobule activation during imagined hand-grip movement. Iacoboni and Zaidel (2004) implicated right superior parietal cortex in visuomotor integration. Adam et al. (2003) identified a very similar set of regions involved in preparing specific finger movements, including intraparietal sulcus and superior parietal lobule as well as several of the motor regions found in our LV1 (middle frontal gyrus, motor cortex, cerebellum and basal ganglia).

The LV1 network observed here may serve these motor attention and performance functions. In the anticipatory (CUE) phase, participants are getting ready for visual stimulus processing, but they are also getting ready to select and make a rapid motor response. During the CUE phase, strong activity within the basal ganglia portions of the network may reflect inhibition of prepared motor behavior during the delay period. During the MOTION phase, participants are viewing a series of 10 stimuli and responding to 1–3 of these stimuli. Thus, in this period, the network activity may reflect motor performance, but also heightened motor preparation, as participants must increase response readiness while viewing the stimuli in order to respond immediately to targets within the motion series. Note, however, that the right-sided laterality we see in parietal regions is inconsistent with Rushworth et al. (2003). Right-sided activity suggests visuospatial attention (see LV2). This might relate to one of a number of differences between our task and that used by Rushworth and colleague's tasks in an important way. In particular, our cued attention, instead of directly cueing the nature of the motor response, cued the relevant side of visual information. This visual information, during the MOTION condition, would eventually lead to motor responses. Thus, the motor attention we required of our participants was

indirect, and relied on visual processing as an intermediary. Apart from the lateralization, the intraparietal sulcus cluster we report here is more medial and slightly more ventral than the center-of-mass coordinates reported by Rushworth et al. (2003). Thus, we cannot precisely localize this type of motor attention to the medial/dorsal bank. Finally, the involvement of the V5/MT+ and V3 seeds in LV1 suggests that this network coordinates its activity with the relevant visual (i.e., moving-stimulus processing) regions.

A visual attention network

The network identified in LV2 involved many visual occipital regions but also bilateral angular gyrus and supramarginal gyrus as well as frontal areas. The frontal–occipital pattern is consistent with top-down attentional control (e.g., Giesbrecht et al., 2003; Hopfinger et al., 2000; Macaluso et al., 2003) as suggested by Luks and Simpson (2004). The angular gyrus and supramarginal gyrus were also reported by Shulman et al. (1999) in a cued attention to motion task and by Luks and Simpson (2004) who suggested their involvement in high-order object processing, i.e., of objects defined by motion (e.g., Schubotz and von Cramon, 2002; Sunaert et al., 1999). A TMS study found the right angular gyrus in particular to be involved in shifting spatial attention (Chambers et al., 2004). As with the network defined by LV1, this network appears to be a composite that includes areas implicated in both cued shifting of visual attention and sustained attention during selective processing of visual information (e.g., Corbetta and Shulman, 1998; Hopfinger et al., 2000; Kastner et al., 1999; Liu et al., 2003; Nobre et al., 2000; Rosen et al., 1999; Shulman et al., 1999; Yantis et al., 2002). The large supramarginal-angular gyrus region could include areas referred to as inferior parietal lobe (IPL) or temporal parietal junction in attention studies (e.g., Corbetta et al., 2000; Serences et al., 2005; Vandenberghe et al., 2001; Yantis et al., 2002). Interestingly, the set of regions in LV2 is correlated with seed activity in many of the regions involved in LV1, and in particular, ventral intraparietal sulcus, both left- and right-sided, which has also been found to activate during anticipatory visuospatial attention (Corbetta et al., 2000).

Preparatory attention throughout the CUE period

The preparatory task investigated here was designed to identify processes involved in preparatory attention to motion stimuli in the absence of stimulation. This task employs relatively long fixation (BASELINE) and preparatory (CUE) periods in order to match the time scale necessary for analysis of the slow BOLD hemodynamic response function. As a consequence, participants could be relaxing their preparatory processes after 1.25 s following the onset of the CUE fixation stimulus, with the knowledge that the motion stimuli will not occur for another 8.5 s. However, due to the slowness of the BOLD response, this would mean that the bulk of the activity included in the analysis from the CUE period contains these early preparatory processes. Thus, our conclusions regarding preparatory deployment of attention processes stand, but they may relate more to these earlier processes rather than preparatory processes present throughout the entire 10-s CUE period.

Multi-seed, cross-condition partial least squares analysis

The novel multivariate method presented here was aimed at uncovering interactions between regions comprising functional networks across phases of a task. By seeding each of the two conditions with seeds from both conditions, we extended the prior seed PLS approach to be able to identify activity that covaried across conditions, precisely the type of activity one expects related to preparatory cognitive processes.

The method is exploratory in the sense that it allows for the possibility of failing to find reliable latent variables, as well as finding only latent variables that miss our hypotheses. For example, it does not necessarily follow from the analysis methodology that the latent variables should include reliable relationships between seed and voxel activity that crosses conditions. That we do in fact obtain such latent variables supports our hypothesis that preparatory attention activity influences subsequent activity of motion-processing regions. We found that CUE seeds covaried with brain LV activity during MOTION, supporting their role in preparatory activity. Because these were found only for LV2, this further specifies their role, suggesting that these VIPS seed areas reflect preparatory activity that influences subsequent activity in visual attention areas but not in visuomotor attention areas (i.e., the LV1 network). Further, both LVs revealed, in the brain LV, areas that covaried with subsequent activity in MOTION seeds. This supports our second hypothesis, namely, that some preparatory activity that influences subsequent motion-stimulus processing is not evident in average activation levels (prior univariate analysis) but the variability of those areas across subjects reflects individual differences in preparatory attention strategy, relating either to visuomotor attention processes (LV1) or visual attention processes (LV2). Beyond supporting our hypotheses, the PLS analysis revealed additional, unpredicted interactions that underscore the complexity of the interactions between brain regions beyond those suggested by current, and necessarily simpler, theories of attention.

It is important to note that the correlation between voxel activity and seeds was performed across subjects. A different approach would have been to perform this correlation across trials, within subjects. However, approaches based on within- and between-subjects variance should converge, as discussed by McIntosh (1999). In the case of estimates derived from within-subjects variance (trial-to-trial), the measures indicate the range of values the functional connections can take in the sample while between-subjects estimate indexes the reliability and direction of the functional connection. Thus, the two approaches may give somewhat different, but not contradictory, views of a functional network. Because single trials are noisy, within-subjects analysis requires more trials per subject than were collected in the present experiment. For this reason, we chose to work with subject averages, which remove much of the single-trial noise.

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