# Parallel Streams to Interconnected Networks: Organization and Reorganization of Cortical Processing During Visual Perception and Action

**Title Page**

**Abbreviated title**: From streams to network

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# Abstract

Dual stream theory of visual processing posits that two distinct neural pathways of specific functional significance originate from primary visual areas and reaches the inferior temporal and posterior parietal areas. However, there are several unresolved questions concerning the fundamental aspects of this theory. For example, is the functional dissociation between ventral and dorsal stream input or output based? Is the dual stream rigid or adaptable to changes? What are the nature of the interactions between ventral and dorsal streams? We addressed these questions using fMRI recordings on healthy human volunteers when they perform perception and action tasks involving color, face, and position stimuli. fMRI scans were repeated after seven practice sessions to investigate the effects of neuroplasticity. Brain mapping analysis supports an input-based functional specialization and existence of context-dependent neuroplasticity in dual stream areas. Intriguingly, premotor cortex activation was observed in position perception task and distributed deactivated regions showing decrease in BOLD activity during task performance compared to baseline was observed in all perception tasks. Dynamic causal modelling (DCM) analysis of cortical activations and deactivations during perception tasks indicates that the brain dynamics in dorsal and ventral stream areas could be interpreted within the framework of predictive coding. DCM analysis also reveals an inhibitory influence from dorsal to ventral stream regions while performing goal-directed action. Effectively, the network level findings point towards the existence of more intricate context-driven functional networks selective of "what" and "where" information processing and likely breakdown of the parallel architecture underlying processing of visual information.


# Significant Statement

The present work addressed several gaps in the visual dual stream theory. The study supported an input-based functional specialization in the dual stream, however, the dominant dual stream theories could not explain the pattern of BOLD activations and deactivations in entirety. Using network metrics we could establish the mechanism of predictive coding as a guiding principle to interpret the brain dynamics in dorsal and ventral stream areas. Effective connectivity analysis during action tasks revealed the inhibitory influence of dorsal areas on to ventral stream processing and demonstrated that this influence consolidated over training. Overall, the study pointed towards the existence of more intricate context-driven functional networks and likely breakdown of the parallel architecture underlying processing of visual information.

# Introduction

The existence of two distinct streams of neural information processing- ventral and dorsal, projecting from the primary visual cortical areas to the inferior temporal cortex and the posterior parietal cortex respectively has been a powerful theory for about last 40 years (Mishkin and Ungerleider, 1982; Goodale and Milner, 1992). Similar duplex architecture in information processing associated with other brain functions e.g., auditory (Romanski et al., 1999), haptic (James and Kim, 2010) and chemosensory perception (Frasnelli et al., 2012), attention (Vossel et al., 2014), speech (Hickok and Poeppel, 2007) and language (Saur et al., 2008) have been subsequently proposed. Despite such importance, several aspects of the visual dual stream theory are still poorly understood, particularly specific roles of individual brain regions in the dual stream pathways, their interactions with each other for processing a putative perception/ action task, and functional reorganization of dual stream with time. We address two prominent issues in the present article.

First, there exists diverging predictions from the two most powerful variations of visual dual stream theory, the Mishkin-Ungerlieder (MU) model (Mishkin and Ungerleider, 1982) and the Milner-Goodale (MG) model (Goodale and Milner, 1992) in terms of functional specialization of the two streams and their interactions. MU model suggests that the *input* information decides the neural pathway for processing. Features that help in object identification ("what") like color, shape, texture etc. are processed in the occipito-temporal or ventral stream whereas perception of spatial ("where") information and spatial (e.g., position, velocity, depth, orientation) take the occipito-parietal or dorsal stream. In contrast, the MG model suggests that the *output* or the task goal decides the processing pathway. The ventral stream areas are needed for internal representation ("perception") of *both* what and where information whereas the dorsal stream is recruited for processing those *same input information* for guiding visuomotor "actions". This hypothesis is supported by the observation that patient DF could insert a card in a slot, which was randomly set at different angles, relative seamlessly, but was unable to correctly describe or otherwise report the orientation of the slot. While both MG and MU, models may predict same brain activation in certain situations (Figure 1.(a),(b)), e.g., ventral stream activation during "perception" of "what" information, nonetheless, the models diverge in activation prediction in situations such as "perception" of "where" information (Figure 1.(c), (d)). Moreover, in some conditions e.g., during "action" task guided by "what" information, (Figure 1.(e),(f)) both the model anticipate activation in the same brain regions but the underlying pattern of flow of information between different brain regions differs. Thus, the first objective of the present work is to critically assess two models of visual dual stream in a single fMRI study.

The second objective of the study is to probe upto what extent the dual stream is subjected to reorganization by learning and familiarity. Longitudinal studies involving patients with visual form agnosia and optic ataxia resulting from ventral or dorsal stream damage, such as the well-known patient DF, have often yielded contradictory observations (Schenk, 2006; V.H. and KR., 2008; Schenk and Mcintosh, 2010; Schenk, 2012; Whitwell et al., 2015). For example, Schenk (2012) reported when haptic feedback was removed DF was unable to insert the card in the target slot which suggests a dissociation of action and perception is unlikely. Contrary to the earlier report, Whitwell et al. (2015) reported that even with removal of haptic feedback, DF was able to seamlessly insert the card in the target slot, essentially emphasizing the dominance of MG model. Since there is a period of 3 years that elapsed between these two studies, the effects of learning in the same patient DF cannot be ruled out while interpreting the contrary reports. Therefore, we hypothesize that parametric control of neuroplasticity introduced in investigations of dual stream dissociation of action-perception can help in reconciling some of these apparently disparate observations. Moreover, if developmental changes to the streams can be tracked, they can then be used to conceptualize a marker to differentiate between normal visuomotor functions and pathological scenarios. Hence, to explore the effects of neuroplasticity driven by behavioral skill development, we performed successive brain scans interspersed by a week of training in perception and action tasks.

# Materials and Methods

## Participants

22 right handed healthy volunteers (14 females, 8 males) were included in the study who declared normal or corrected-to-normal vision with no history of neurological/ neuropsychiatric ailments. Two of the volunteer's data were excluded due to excessive head movement inside the scanner. Mean age was 25.35 years (SD =2.796) in the final analysis. Handedness were tested according to the Edinburgh Inventory. All participants gave written informed consent to the experimental procedure, the format of which was approved by the Institutional Human Ethics Committee of National Brain Research Centre (IHEC, NBRC) and in agreement with the Declaration at Helsinki.

## Experimental Design, Stimuli, and Tasks

We designed an experimental paradigm that aims to reveal the brain activations along ventral and dorsal processing pathways in context of attributes color, face and position (Figure 2). Two kinds of tasks were designed:

1. *Perception* tasks: Color perception was studied using four different colored filled circles that were presented one at a time randomly but consecutively and then participant was asked to report verbally the number of times the target color (red) were presented in a run. Similarly, in face perception task, four different faces were randomly presented one at a time and the task was to indicate the number of times a particular target face was presented. In position perception trials, two black dots were presented in different positions with respect to the central cross in the screen, and the task was to calculate and report the number of times the two dots were equidistant from the central cross. In all three kinds of contexts, stimuli were presented at the centre of the screen. In order to minimize eye movements and cued saccades during position perception tasks, the location of two black dots were restricted within the foveal vision (3 degrees of visual angle) of each participant. Visual angle extended by color stimuli and face stimuli were also 3 degrees. Stimuli were presented using Presentation software (Version 18.0, Neurobehavioral Systems, Inc.,

Berkeley, CA; www.neurobs.com).

2. Visually-guided *action* tasks: Participants were asked to move the cursor on the screen with the help of an fMRI compatible joystick (Current Designs, Inc.; Model HHSC-JOY-5; http://curdes.com) whose movement was calibrated to match the velocity and direction of the cursor movement to a target stimulus. Red circle, a target face, or the distant black dot from the centre of the screen were the target stimuli among two dissimilar stimuli of the same category presented simultaneously (Figure 2).

Visual stimuli for both perception and action tasks were presented with a grey background in eight "On" blocks (duration 24 seconds each) alternating with "Off" blocks of 16 seconds duration (Figure 2). During Off blocks a central cross on a grey background was presented. 8 On and Off blocks (1 run) of each attribute were presented successively. In perception tasks, each stimulus was presented for one second (with no interstimulus interval) while in action tasks each stimulus persists until the participants move the cursor to the target location. However, if the participant had failed to move the cursor to the target within a window of 4s, the next set of visual objects would appear immediately. For perception tasks, the number of times a target attribute appeared were reported by participants verbally after the completion 1 run. For action tasks, the number of times the stimulus appeared within each On block depended on the performance of participants.

To assess the effects of learning onto dual-stream visual processing pathways, participants were trained in the aforementioned tasks for 7 consecutive days in a non-MRI environment following the first fMRI scan session. Each practice session comprised of same six tasks identical to scanning sessions but the order of presentation of individual stimuli within a task were randomized for each of the sessions. The order of six task blocks were also randomized. The number of practice sessions were decided based on a pilot study probing the improvement of response time with practice. From eighth days the performance saturated in the pilot sessions.

## MRI Data Acquisition

Images were acquired on a 3T (Philips Achieva) Magnetic resonance imaging (MRI) scanner at NBRC using a standard whole head coil (8-channels). To limit head movement related artifacts, participants were verbally instructed to keep their heads as still as possible. Additionally, the participant's head was fixed by foam padding. Ear plugs and customized headphones were used to attenuate scanner noise. The room lights were dimmed at near-identical levels for all participants.

*Structural MRI*: High-resolution T1-weighted structural MRI images with repetition time (TR)= 8.4 ms, echo time (TE)=3.7ms, flip angle (FA) = 8 degrees, matrix = $252 \times 230 \times 170$, field of view (FOV) = $250 \times 230 \times 170$ mm were acquired from each participant for anatomical coregistration.

*Functional MRI*: T2* weighted functional whole-brain images were acquired with TR= 2000 ms, TE= 35 ms , FA = 90 degrees, matrix = $60 \times 62 \times 30$, FOV = $230 \times 230 \times 179$ mm during each task performance using a gradient echo-planar imaging (EPI) sequence.

## Behavioural Data Analysis

For perception tasks, verbal response was sought from participants after each run to report the number of times the target stimulus were presented. For visually guided action tasks, the response time (RT) was computed by measuring the time taken by the participant to move the cursor to the target object after two objects change position. Two way ANOVA was employed to compare RTs across days and tasks. Post hoc Tukey-Kramer test was also used to compare RTs in all possible pairs of conditions.

## Preprocessing and brain activation mapping

The preprocessing and statistical analysis of fMRI data were executed with SPM8 toolbox (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm/). Initial 8 seconds of scanning sequence were discarded to allow the magnetization to stabilize to a steady state. Prior to statistical analysis, images were slice-time corrected, realigned with the mean image, motion corrected, coregistered with the corresponding T1-weighted images, normalized to a Montreal Neurological Institute (MNI, https://www.mcgill.ca/) reference template and resampled to $4 \times 4 \times 5$ mm$^3$. During motion correction 2nd degree B-Spline interpolation was employed for estimation and 4th degree B-Spline for reslicing. Coregistration used mutual information objective function while normalization used 4th degree B-Spline interpolation. Temporal high pass filtering with cut off of 128 seconds was employed to remove low frequency drifts caused by physiological and physical (scanner related) noises. Images were smoothed with a full-width at half-maximum (FWHM) Gaussian kernel $8 \times 8 \times 10$ mm$^3$.

The general linear model (GLM) based one-sample t test was employed to identify brain activations and deactivations (Friston et al., 1994). The design matrix included regressors of interest for each task representing the event onsets and their time course as well as realignment parameters for head movement as regressors of no interest. The resulting statistical parametric maps of the t-statistics for contrast $Task - Baseline$ were thresholded at $p < 0.01$ (False Discovery Rate: FDR corrected) to get the activated voxels at each participant-level across the whole brain. Group analyses were performed using a random effects model. Deactivated voxels during tasks were identified by implementing a GLM with contrast $Baseline - Task$ and repeating the aforementioned steps. Anatomical localization of local maxima of activation / deactivation was assessed using the SPM Anatomy toolbox (v 2.2b, Eickhoff et al. 2005).

Subsequently, we were interested in tracking the number of activated/ deactivated voxels as well as the percentage signal change in dual stream areas between two scanning sessions interspersed with practice sessions. V1-V2 mask was created by combining BA17 and BA18 masks, ventral stream (VEN) mask by combining ventral extrastiate cortex, lateral occipital cortex, and gyrus fusiformis and dorsal stream (DOR) mask by combining dorsal extrastiate cortex, V5/MT+, inferior parietal cortex, intraparietal sulcus, and superior parietal cortex. Probabilistic cytoarchitectonic maps from SPM Anatomy toolbox (Eickhoff et al., 2005) were used as masks for ROI computation. Comparison between 2 scanning sessions were done Wilcoxon signed rank test.

## Dynamic causal modeling

A deterministic bilinear variant of Dynamic causal modelling (DCM) (Friston et al., 2003) was employed to probe the effective connectivity among the activated / deactivated regions. Alternative models were compared by Bayesian model selection, that rests on computing the model evidence, i.e., the probability of the data (BOLD signal) given a specific model. The posterior probability of coupling parameters is estimated by Bayesian Model Averaging (BMA), where we average over models, weighted by posterior probability of each model. Effective network models were constructed for activation and deactivation separately in each hemisphere in the region of interests (ROI). Different network schemas involving primary visual cortex (V1), ventral extrstriate areas (VES), fusiform gyrus (FG), dorsal extrastriate areas (DES), superior parietal lobule (SPL), premotor cortex (PMC), and motor cortex (Mot) as ROIs were chosen as nodes of "activation" and "deactivation" networks in a respective task category.

*Time series extraction*: Time series for DCM analysis were extracted by taking the first principal component of the time series from all voxels included in a sphere of 6 mm diameter centered on the peak activated voxel in each participant. We also adjust data for "Effects of interest" thus effectively mean-correcting the time series.

*Model space construction*: DCMs for activation networks in color and face perception tasks included bilateral intrinsic connectivity between primary visual cortex (VIS) and extrastriatal ventral stream (VES), as well as between VES and fusiform gyrus (FG) and no direct intrinsic connectivity between VIS and FG. The recurrent or self connections were also considered (Figure 3(a)). Two kinds of model families were considered, in both of which visual inputs enter the system via primary visual cortex. However, in model 1, only the feed-forward connections , i.e., from VIS to VES and from VES to FG are modulated, whereas in model 2 both feed-forward and feedback connections including from FG to VES and from VES to VIS are modulated. Analogously, DCMs for activation networks during position perception involved SPL and PMC. Here, two alternative models have bilateral intrinsic connectivity between both nodes and self connections and inputs enter the system at SPL (Figure 3(c)). In model 1, only the causal connections from SPL to PMC is modulated whereas in model 2 connections are modulated in both directions. DCMs for deactivation networks (observed for perception tasks only) have bidirectional intrinsic connectivity among nodes in the immediate hierarchy (V1-DES and DES-SPL) and self connections simultaneously (Figure 3(b)). Out of the two models tested, model 1 had only the self connections modulated whereas in model 2, input enters the system via SPL and all other top down connections (SPL $\rightarrow$ DES, DES $\rightarrow$ VIS) are modulated by the tasks.

Only activation networks are relevant for action tasks and we consider models consisting of four ROIs - V1, FG (ventral stream area), SPL (dorsal stream area) and motor cortex (Figure 3(d)). In all models visual inputs enters the models via primary visual cortex. All the nodes are intrinsically connected among each other except primary visual cortex and motor cortex between which there is no direct intrinsic connection. We consider modulation of all non-self connections between nodes. A “full” model in which all non-self connections are modulated is represented in Figure 3(d). Other models are constructed based on modulation of combinations of effective connections between four nodes. One such model with modulation of 5 connections is also shown in the same figure. In total, 80 models were evaluated for model evidence computation.

# Results

## Behavioral performance and effects of practice

All participants were 100 % accurate in counting the number of target stimuli that were presented in each block during perception tasks, during both scanning sessions and for the 7 practice sessions. Response times (RT) were computed trial-by-trial in visually guided action tasks (Figure 4). Two way ANOVA on RT with task category (color, face, or position action) and training days as variable shows significant main effect of both practice, $p < 0.0001$ (deg of freedom $= 8$), and task condition $p < 0.0001$ (deg of freedom $= 2$), on RT with no significant interaction effect, $p = 0.5004$ (deg of freedom $= 16$). In general, color action shows the fastest and position action the slowest response time. Compared to last practice session, Response time deteriorates in 2nd fMRI scan. Post-hoc analysis with Bonferroni multiple comparison revealed that RT in 2nd fMRI scan session is significantly faster than RT in 1st fMRI scan session (p=0.0029).

## Mapping functional brain activity along dual stream: SPM results

### Activation and deactivation of dorsal and ventral visual areas in perception tasks

Significant activations were observed along primary visual areas (V1 and V2) and along the ventral stream, V3v, V4v, lateral occipital complex (LOC), and fusiform gyrus (FG) during color and face perception tasks for both scanning sessions, day 0 (scan 1) and day 8 (scan 2), separated by 7 practice days (Figure 5, Table 1).

In position perception task (Figure 5, Table 1), bilateral ventral(e.g, V4v, LOC, FG) , and dorsal (e.g.,V5/MT, SPL ) stream regions were activated for both scan 1 and 2. Bilateral premotor cortex (PMC) also show activation in both the scans. Interestingly, primary and secondary visual cortices did not exhibit activations in either scan at the FDR-corrected group level analysis.

Subsequently, the outcome of Wilcoxon signed ranked tests performed for number of activated/ deactivated voxels were reported in Table 2 (detailed descriptions for each scanning session is presented in extended data 2-1). Similarly, results from Wilcoxon signed ranked tests performed on the percentage signal change comparisons between scan 1 and scan 2 were presented in Table 3 (individual percentage signal changes in each scan sessions are reported in extended data 3-1). A general trend of decrease in the extent of activation in ventral and dorsal stream in all perception tasks emerges from comparisons between scan 1 and 2. However, percentage signal change between scanning sessions rarely changed.

Intriguingly, all perception tasks showed distinct areas of deactivation (relative to control block) at the group level (Figure 5,Table 1). The deactivated areas predominantly involved bilateral primary and secondary visual cortices, and dorsal stream regions (extrastriate dorsal stream, superior parietal lobule). Certain ventral stream regions such as extrastriate ventral stream and fusiform gyrus also show some deactivation. Compared to activated areas in perception (and response) tasks, the deactivated areas are located more medially. In contrast to activation, there were no statistically significant change in the extent of deactivation between scan 1 and scan 2 (except dorsal stream deactivation in face perception) (Table 2, 2-1).

### Activation of dorsal and ventral stream areas in action tasks

In all action tasks (Figure 5, Table 1) primary and secondary visual cortices, ventral and dorsal stream areas and motor cortex undergo bilateral activation in both scan 1 and 2. There is a decrease in the extent of activation, however, the statistically significant decrease during scan 2 predominantly occurs in the right hemisphere (Table 2, 2-1). Analogous to perception tasks, percentage signal change does not show significant change with practice in scan 2 (Table 3, 3-1) compared to scan 1. Unlike perception tasks, there is no significant deactivation in any of the action tasks, in both scan 1 and 2.

## Brain network analysis

After identifying activation and deactivation of several brain regions in perception task and primarily activation in those regions during action task, we tried to underpin the effective connectiviy between these regions across tasks, and their alteration with practice. To address these systematically, we employ Dynamic causal modelling (DCM) to evaluate effective brain networks underlying perception and action tasks according to the scenarios proposed in Fig 3.

### Perception tasks

DCM was applied to evaluate the intricate causal relationships in the "activation" and "deactivation" networks among the participants (see Methods for details) with primarily two classes of models being tested. Model 1 represented bottom-up sensory driven processing circuit for activation networks and self-modulating network nodes for deactivation networks. On the other hand, model 2 always represented a network scheme that involves top-down information transfer with or without the bottom-up processing.

For activation networks during color, face and position perception, model 2 schemas are more likely candidates that facilitate the underlying information processing (see Figure 6 a and b). Subsequently, on parameter estimation (see Figure 6-2), all the feed-forward connections among activated regions were found to be positive whereas feedback connections were negative. Scan 1 and scan 2 had same pattern of causal interactions along with similar strength of effective connections.

DCM on the time series from deactivated brain areas also favor model 2. The input to SPL was found to be inhibitory whereas the coupling parameter of feedback connections between deactivated regions were estimated to be positively modulated during each perception tasks, across scanning sessions 1 and 2.

### Effective connectivity in action tasks

DCM analysis of *action* tasks required comparison among 80 different models (Fig 3 d). On estimating the coupling parameters, we found that primary visual cortex positively influences ventral and dorsal regions as predicted by dual stream theory in all action tasks (see Figure 6 c-h). Both the ventral region (FG) and dorsal region (SPL), in turn, positively influence the motor cortex to perform the visually guided actions tasks cued with face and color stimuli. In position action tasks, motor cortex is driven by FG but not SPL, whereas in color-cued and face-cued action tasks before practice motor cortex is driven by SPL. The feedback connections (FG $\rightarrow$ V1, SPL $\rightarrow$ V1, MOT$\rightarrow$ FG, MOT $\rightarrow$ SPL), when present, are all inhibitory. There is also strong inhibitory influence from dorsal stream regions to ventral stream regions while performing the movement and this inhibitory influence either remains same (for position action task) or is enhanced (for color and face action) with practice as reflected in the estimated coupling parameters.

# Discussion

Our study aimed to investigate the subtle variants of visual dual stream theory proposed by Mishkin-Ungerlieder (MU) (Mishkin and Ungerleider, 1982; Mishkin et al., 1983) and Milner-Goodale (MG) (Goodale and Milner, 1992; Milner et al., 2012), on a task ideally designed to validate their respective predictive power in understanding and interpreting patterned brain activity. Accordingly we conceptualized two kinds of tasks - one that involved perception of visual objects (*perception* tasks), e.g., color, face or position stimuli in absence of any motor goal and the other which required performance of goal directed movements (*action* tasks) with a joy-stick following color, face or position cues. MU model would predict only dorsal stream activations for position stimuli but ventral stream activations for color and face stimuli in perception tasks. On the other hand, MG model would predict the involvement of only ventral areas in all perception tasks. Intriguingly, we see both dorsal and ventral stream activations in position perception tasks, an observation that diverges from predictions of both the models. Secondly, we observed patterned deactivation in dorsal and ventral stream brain regions for color/ face and position stimuli respectively. Thirdly, the activation and deactivation in perception and action tasks showed changes in the pattern depending on the context of the tasks. Fourthly, using dynamic causal modelling (DCM) (Friston et al., 2003) we could demonstrate how predictive coding may be relevant for understanding the role of top-down modulations in higher order visual areas during perception-action tasks and how "cross-stream" inhibitory influences are exerted by dorsal stream regions onto ventral stream areas during action tasks. With training, the inhibitory influences either remain same or get consolidated to an unidirectional dorsal to ventral influence. Recently, increasing evidence have shown that the ventral and dorsal streams are not strictly independent, but do interact with each other directly (for a review see van Polanen and Davare (2015)). However, this is the first study, to the best of our knowledge, to point out that the nature of dorsal to ventral influence may be inhibitory and demonstrate the evolution of such interactions with training. Based on all these observations, we propose a revision of stream-based models to a more nuanced network-level understanding of visual information processing that show context-dependent neuroplasticity over time.

BOLD deactivation is relatively a rarely discussed topic and often looked upon with suspicion by the neuroimaging community. More often than not it is explained by the so-called "blood stealing" effect - redirection of blood flow to the activated region and away from adjacent inactive regions, and routinely ignored (Wade, 2002; Hayes and Huxtable, 2012). Nonetheless, the deactivation found during the perception tasks in the present study is consistent across tasks and practice sessions, is much more extensive compared to the activation (at least in color and face perception), and includes too many distal regions than the activated areas to share a common pool of blood supply. Thus, neuronal suppression is a more probable explanation for the deactivations we observed in this study in contrast to blood stealing (Frankenstein et al., 2003).

The decrease in the number of activated voxels in perception and action tasks with practice reflects the habituation effect, a form of neuroplasticity marked by the progressive decrease of the responses to repeated sensory stimulation (Glaser and Whittow, 1953). In action tasks, the lateralization of contraction of activated regions denotes that the habituation in dual stream is dependent on context e.g., right-handedness of the participants in the present study. Preservation of overall activation pattern, constancy of percentage signal change in the face of contraction and lowering of reaction time supports the idea that habituation effectuates a more efficient processing of information which consumes a lesser amount of energy reflected by a decrease in the spatial boundaries of activation patterns (Kok et al., 2012).

The predictive coding framework, an emerging theory of brain function, suggests that the brain is continually attempting to predict the external causes of sensory information at all levels of the cortical processing hierarchy (Mumford, 1992; Rao and Ballard, 1999; Friston and Kiebel, 2009). According to the most recent variation (Friston and Kiebel, 2009) of this view, feedback connections from a higher- to a lower-order sensory cortical area carry predictions of lower-level neural activities and inhibit/explain away the predicted signal in the lower level. The residual error, if any, is carried by the feed-forward connections, which is excitatory in nature, and which updates the prediction at the higher level. This process continues until prediction matches the incoming stimuli. This view represents a more computationally efficient alternative to traditional model of sensory processing where each feature of the sensory object is processed and integrated in a predominantly bottom up direction. In other words, lower order areas act as filter to ignore redundancy in signal based on a prediction code. In our present study, we found feed-forward connections among activated regions in perception tasks to be contributing towards excitatory “influences" while feedback connections contributing to inhibitory “influences" (see Figure 6(a)) thus complying with the variation of predictive coding theory proposed by Friston and Kiebel (2009).

Similarly, neural suppression in dorsal stream in perception tasks were found to be mediated by top-down inhibitory influence. A possible explanation of deactivation in dorsal stream is repetition/expectation suppression (RS or ES) (Meyer and Olson, 2011; Grill-Spector et al., 2006) as in all perception tasks stimuli were presented centrally in the same location. As the stimuli location is fully predictable, there is no feedforward prediction error. On the other hand, as the subject concentrate to perceive the stimuli, the top-down inhibitory influence of prediction increases during active blocks. Thus resulting in overall deactivation compared to rest blocks. This explanation of prediction/repetition suppression which is based on predictive coding and is supported by our analysis contradicts a more traditional explanation that bases on local mechanisms such as fatigue (Grill-Spector et al., 2006) that can be represented self-inhibiting loops to a neuronal population so that the inhibition is proportional to the neuronal activity ( DCM 2 in our analysis).

The DCM analysis shows a consistent inhibitory influence of SPL to FG during action tasks. There is already a few papers emphasizing the interaction between ventral and dorsal stream during task performance (Himmelbach and Karnath, 2005; van Polanen and Davare, 2015). However, to our knowledge, this is the first work to point out the nature of dorsal to ventral influence to be inhibitory. The interaction between two streams also lends support to the conceptualization of visual brain as a network ( for a review see Schenk and Mcintosh (2010) ) as opposed to two functionally independent streams.

Interestingly, the strengthening of the inhibitory influence over practice corresponds to the improvement of the response time in action tasks. However, to ascertain the exact role of this inhibitory influence, and the reason behind its strengthening would be merely speculative at this stage and must be left as the questions for future research. Electrophysiological study (including micro-electrode recordings from primate) could provide insight into the neurophysiological basis of the inhibitory influence by exploring the temporality of ventral and dorsal stream activity. Transcranial magnetic stimulation (TMS) study could be explored as an alternative approach in human participants. Specific brain regions in ventral or dorsal stream could be stimulated while performing visuomotor tasks and its effect on the behavior (response time, accuracy) could be studied in the near future.

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# Legends

## Tables

**Table 1.** Local Maxima of BOLD activity at Group Level Analysis

**Table 2.** Wilcoxon signed rank test: No. of activated and deactivated voxels: Before and After Practice

**Table 3.** Wilcoxon signed rank test: Percentage Signal Change: Before and After Practice

## Figures

**Figure 1.** Predictions of brain activation by two models of dual stream theory in different tasks. (a), (b) During perception of what information (e.g., color perception) both models predict activation of ventral stream regions but follow different rationale based on input and output level explanations, respectively. (c), (d) During perception of where information (e.g., perception of position), however, the predictions of two models diverge. (e),(f) For what information guided action tasks (e.g., reaching to a particular color target), though activation of primary visual areas, ventral and dorsal stream regions, and motor cortex is predicted by both the models, speculation about the flow of information between these regions is different. Particularly, according to MG model, dorsal stream is independently capable of processing both what and where information for guiding action in motor cortex. Thus, though there is flow of information from primary visual cortex to ventral stream regions, as there is simultaneous internal representation of visual information while performing the action, the flow from ventral stream to motor cortex is redundant.

**Figure 2.** Experimental paradigm. In the perception tasks ((a),(b), and (c)) the participants were asked to calculate the number of times target stimuli ( red dot, target face, equidistant black dots) were presented. In action tasks ((d),(e),and (f)) they were instructed to move the cursor in the screen with the help of a joystick to the target stimuli (red dot, target face, distant black dot) among two simultaneously presented stimuli in each trial. Each trial was presented for 1 seconds in

perception tasks and till the cursor reach the target (unless it is more than 4 seconds) in the action tasks. Stimuli were presented in active blocks of 24 seconds duration alternating with 16 seconds rest blocks. Each task run consists of such 16 alternating blocks. Presentation of the tasks for each participants and presentation of the stimuli within each block were randomized.

**Figure 3.** Model space. For each of (a) ventral stream activation, and (b) dorsal stream deactivation in color and face perception, and (c) dorsal stream and premotor cortex activation in position perception tasks, two competing models were compared. Primary visual cortex (V1), extrastriate ventral stream regions (VES), and fusiform gyrus (FG) consisted the regions of interests (ROIs) for (a), and V1, extrastriate dorsal stream regions (DES), and superior parietal lobule (SPL) consisted the ROIs for (b). For (c) connections between the SPL and premotor cortex (PMC) were analysed. For each of (a), and (b), intrinsic connections were assumed between ROIs in immediate hieararchy, and self loops whereas for (c) all possible intrinsic connections between SPL and PMC, and self-loops were assumed. Among the two models for (a),(b),and (c) the first model has only modulation of feedforward connections while the second model also has modulation of feedback connections. For (d) activation in action tasks connectivity between V1, FG, SPL, and primary motor cortex (Mot) was considered. We assumed to have no direct intrinsic connection between V1, and Mot, otherwise all possible connections including self loops were considered. All possible modulation of non-self connections gave rise to 80 different competing models. For illustration, a full model with modulation of all non-self connections and another model with modulation of 5 connections were depicted.

**Figure 4.** Behavioural result. Group level Mean and SD of response times in color, face, and position action tasks across scanning and practice sessions.

**Figure 5.** Brain activation and deactivation in perception and action tasks.

**Figure 6.** Effective connectivity: (a) Cartoon figures representing general patterns of nature (positive modulation: red, negative modulation: blue) of modulation of connections (based on estimated coupling parameters) in color and face, and position perception tasks. The nature of modulation does not change with practice. (b) Action tasks. Before and after practice. Color of

the arrow represents the nature (same as perception tasks), and thickness of the arrow represents the value of the coupling parameter for modulation of effective connectivity.

## Extended data

**Table 2-1.** No of voxels activated/deactivated during Perception and Response tasks. V1V2-primary and secondary visual cortex, VEN-ventral stream, DOR-dorsal stream, PMC-premotor cortex, MOT-primary motor cortex.

**Table 3-1.** Percentage signal change during Perception and Response tasks. V1V2-primary and secondary visual cortex, VEN-ventral stream, DOR-dorsal stream, PMC-premotor cortex, MOT-primary motor cortex.

**Figure 6-1** Model comparison: Model expected probability of competing models.

**Figure 6-2** Coupling parameter estimation in perception tasks

# Tables

Table 1

| | BRAIN REGIONS (Right) | T | BRAIN REGIONS (Left) | T |
|---|---|---|---|---|
| **Color Perception: Before Practice** | | | | |
| Activation | LOC | 9.15 | V3v | 8.35 |
| | V1 | 7.88 | | |
| | V3v | 6.3 | | |
| | FG | 9.12 | | |
| Deactivation | V2 | 8.55 | V3v | 8.39 |
| | V3v | 9.11 | V3d | 7.38 |
| | V3d | 6.73 | SPL | 6.78 |
| **Color Perception: After Practice** | | | | |
| Activation | V1 | 6.67 | V3v | 8.04 |
| | V3v | 7.18 | | |
| Dectivation | V1 | 7.51 | V1 | 8.42 |
| | V2 | 7.21 | V2 | 7.81 |
| | V3v | 7.16 | V3v | 6.72 |
| | V3d | 7.36 | | |
| | FG | 6.21 | | |
| **Face Perception: Before Practice** | | | | |
| Activation | V3v | 10.7 | V4v | 11.62 |
| | V4v | 9.09 | LOC | 11.85 |
| | FG | 12.03 | FG | 8.51 |
| Deactivation | V1 | 11.19 | V1 | 9.49 |
| | V2 | 11.15 | V3v | 15.01 |
| | V3d | 11.85 | V3d | 9.34 |
| | SPL | 8.06 | SPL | 7.49 |
| | OP4 [PV] | 6.17 | | |
| **Face Perception: After Practice** | | | | |
| Activation | V3v | 14.39 | V3v | 11.38 |
| | FG | 10.4 | LOC | 8.52 |
| | | | FG | 9.97 |
| Deactivation | V2 | 11.5 | V3v | 10.24 |
| | V3A | 11.14 | V3d | 7.26 |
| | FG | 7.97 | V3A | 8.1 |
| | | | FG | 7.35 |
| **Position Perception: Before Practice** | | | | |
| Activation | V4v | 7.99 | LOC | 6.67 |
| | LOC | 7.65 | V5/MT | 11.18 |
| | FG | 12.12 | SPL | 11.23 |
| | SPL | 11.09 | Area 2 | 9.81 |
| | Area 1 | 9.56 | | |
| | Area 2 | 11.32 | | |
| | Area 44 | 10.82 | | |
| | Lobule VIIb | 6.87 | | |
| Deactivation | V1 | 9.2 | V3v | 6.92 |
| | V2 | 9.26 | V3d | 8.62 |
| | V3v | 8.49 | | |
| | V3A | 10.76 | | |
| | IPL | 7.61 | | |
| | Area TE 1.0 | 8.79 | | |
| **Position Perception: After Practice** | | | | |
| Activation | V4v | 8.04 | V4v | 7.95 |
| | FG | 9.34 | SPL | 10.54 |
| | IPS | 10.59 | Lobule VIIIa (Verm) | 6.18 |
| | SPL | 8.31 | | |
| | Area 2 | 9.46 | | |
| | Area 44 | 7.32 | | |
| Deactivation | V1 | 17.98 | V1 | 12.74 |
| | V2 | 12.05 | V2 | 12.05 |
| | FG4 | 7.89 | V4v | 8.33 |

Table 1: continued

| | BRAIN REGIONS (Right) | T | BRAIN REGIONS (Left) | T |
|---|---|---|---|---|
| Color Action: Before Practice | | | | |
| Activation | V1 | 9.72 | V3v | 12.12 |
| | LOC | 8.99 | V4v | 10.25 |
| | FG | 16.39 | FG | 14 |
| | SPL | 11.95 | SPL | 11.23 |
| | Lobule VI (Hem) | 11.75 | 4a | 10.14 |
| Color Action : After Practice | | | | |
| Activation | V1 | 14.69 | V1 | 10.62 |
| | IPS | 8.63 | V3v | 11.04 |
| | SPL | 8.6 | V5/MT | 10.69 |
| | Lobule V (Hem) | 14.21 | FG | 12.93 |
| | Lobule VI (Hem) | 14.16 | SPL | 0 8.94 |
| | | | 4a | 12.51 |
| | | | 4p | 13.74 |
| | | | Thal: Prefrontal | 8.74 |
| Face Action: Before Practice | | | | |
| Activation | V3v | 13.55 | LOC | 15.38 |
| | V4v | 14.69 | FG | 14.58 |
| | LOC | 14.87 | SPL | 13.94 |
| | FG | 13.24 | 4p | 14.2 |
| | IPS | 13.2 | Thal: Prefrontal | 8.29 |
| | Lobule VI (Hem) | 13.58 | | |
| | Thal: Prefrontal | 7.69 | | |
| Face Action : After Practice | | | | |
| Activation | V1 | 10.35 | V3d | 6.33 |
| | V2 | 10.43 | V5/MT | 10.04 |
| | V3v | 10.64 | LOC | 17.66 |
| | IPS | 10.13 | 4a | 17.29 |
| | SPL | 7.43 | Lobule VI (Hem) | 15.94 |
| | Lobule VI (Hem) | 14.2 | Thal: Prefrontal | 10.08 |
| Position Action: Before Practice | | | | |
| Activation | V1 | 13.11 | V4v | 12.73 |
| | FG | 14.66 | SPL | 15.11 |
| | IPL | 6.13 | 4a | 12.03 |
| | Area 2 | 12.21 | Lobule VI (Hem) | 11.99 |
| | Area 44 | 7.85 | Thal: Prefrontal | 6.55 |
| | Lobule VI (Hem) | 12.04 | Thal: Parietal | 6.1 |
| Position Action : After Practice | | | | |
| Activation | V1 | 10.83 | LOC | 11.05 |
| | V2 | 9.77 | V5/MT | 10.34 |
| | SPL | 11.03 | SPL | 13.43 |
| | Area 2 | 8.16 | Area 1 | 8.42 |
| | Area 44 | 8.63 | Lobule VI (Hem) | 14.34 |
| | Lobule VI (Hem) | 13.67 | Thal: Prefrontal | 8.2 |
| | Thal: Prefrontal | 6.18 | Thal: Motor | 6.53 |

Table 2

Left Hemisphere

| | Activation/ Dactivation | Task | BRAIN REGIONS | p |
|---|---|---|---|---|
| Perception | Activation | Color Perception | V1V2 | 0.1437 |
| | | | *Ven* | *0.0303* |
| | | Face Perception | V1V2 | 0.9036 |
| | | | Ven | 0.0543 |
| | | Position Perception | V1V2 | 0.1914 |
| | | | *Ven* | *0.0032* |
| | | | *Dor* | *0.0028* |
| | | | *PMC* | *0.0006* |
| | Dectivation | Color Perception | V1V2 | 0.7403 |
| | | | Dor | 0.6981 |
| | | Face Perception | V1V2 | 0.0929 |
| | | | *Dor* | *0.0382* |
| | | Position Perception | V1V2 | 0.1840 |
| | | | Dor | 0.1774 |
| Response | Activation | Color Response | V1V2 | 0.6813 |
| | | | Ven | 0.5379 |
| | | | Dor | 0.2110 |
| | | | Mot | 0.8089 |
| | | Face Response | V1V2 | 0.3905 |
| | | | Ven | 0.0702 |
| | | | *Dor* | *0.0438* |
| | | | Mot | 0.6009 |
| | | Position Response | V1V2 | 0.2110 |
| | | | Ven | 0.2470 |
| | | | Dor | 0.4897 |
| | | | Mot | 0.9198 |

Right Hemisphere

| | Activation/ Dactivation | Task | BRAIN REGIONS | p |
|---|---|---|---|---|
| Perception | Activation | Color Perception | *V1V2* | *0.0084* |
| | | | *Ven* | *0.0222* |
| | | Face Perception | V1V2 | 0.2348 |
| | | | Ven | 0.1124 |
| | | Position Perception | V1V2 | 0.9065 |
| | | | *Ven* | *0.0045* |
| | | | *Dor* | *0.0090* |
| | | | *PMC* | *0.0008* |
| | Dectivation | Color Perception | V1V2 | 0.7403 |
| | | | Dor | 0.8129 |
| | | Face Perception | V1V2 | 0.0793 |
| | | | *Dor* | *0.0169* |
| | | Position Perception | V1V2 | 0.1386 |
| | | | Dor | 0.1588 |
| Response | Activation | Color Response | V1V2 | 0.9256 |
| | | | Ven | 0.0859 |
| | | | *Dor* | *0.0057* |
| | | | Mot | 0.5089 |
| | | Face Response | V1V2 | 0.5016 |
| | | | *Ven* | *0.0064* |
| | | | *Dor* | *0.0014* |
| | | | Mot | 0.6009 |
| | | Position Response | V1V2 | 0.2789 |
| | | | *Ven* | *0.0290* |
| | | | *Dor* | *0.0438* |
| | | | Mot | 0.9198 |

Table 3

Left Hemisphere

| | Activation/ Dactivation | Task | BRAIN REGIONS | p |
|---|---|---|---|---|
| Perception | Activation | Color Perception | V1V2 | 0.2959 |
| | | | *Ven* | *0.0045* |
| | | Face Perception | V1V2 | 0.2471 |
| | | | Ven | 0.3317 |
| | | Position Perception | Ven | 0.1790 |
| | | | *Dor* | *0.0111* |
| | | | *PMC* | *0.0045* |
| Perception | Dectivation | Color Perception | V1V2 | 0.6813 |
| | | | Dor | 0.3905 |
| | | Face Perception | V1V2 | 0.0930 |
| | | | Dor | 0.3703 |
| | | Position Perception | V1V2 | 0.1672 |
| | | | Dor | 0.2959 |
| Response | Activation | Color Response | V1V2 | 0.7089 |
| | | | Ven | 0.2322 |
| | | | Dor | 0.1913 |
| | | | Mot | 0.5503 |
| | | Face Response | V1V2 | 0.3135 |
| | | | *Ven* | *0.0333* |
| | | | Dor | 0.1354 |
| | | | Mot | 0.9405 |
| | | Position Response | V1V2 | 0.2180 |
| | | | Ven | 0.1005 |
| | | | Dor | 0.4553 |
| | | | Mot | 0.7369 |

Right Hemisphere

| | Activation/ Dactivation | Task | BRAIN REGIONS | p |
|---|---|---|---|---|
| Perception | Activation | Color Perception | V1V2 | 0.8813 |
| | | | Ven | 0.2627 |
| | | Face Perception | V1V2 | 0.8228 |
| | | | Ven | 0.2043 |
| | | Position Perception | Ven | 0.2180 |
| | | | *Dor* | *0.0276* |
| | | | *PMC* | *0.0124* |
| Perception | Dectivation | Color Perception | V1V2 | 0.5755 |
| | | | Dor | 0.9405 |
| | | Face Perception | V1V2 | 0.0793 |
| | | | Dor | 0.9405 |
| | | Position Perception | V1V2 | 0.6274 |
| | | | *Dor* | *0.0169* |
| Response | Activation | Color Response | V1V2 | 0.4553 |
| | | | *Ven* | *0.0366* |
| | | | Dor | 0.0930 |
| | | | Mot | 0.5503 |
| | | Face Response | V1V2 | 0.3507 |
| | | | *Ven* | *0.0400* |
| | | | *Dor* | *0.0152* |
| | | | Mot | 0.9405 |
| | | Position Response | V1V2 | 0.0859 |
| | | | *Ven* | *0.0111* |
| | | | Dor | 0.0859 |
| | | | Mot | 0.7369 |

538 # Figures

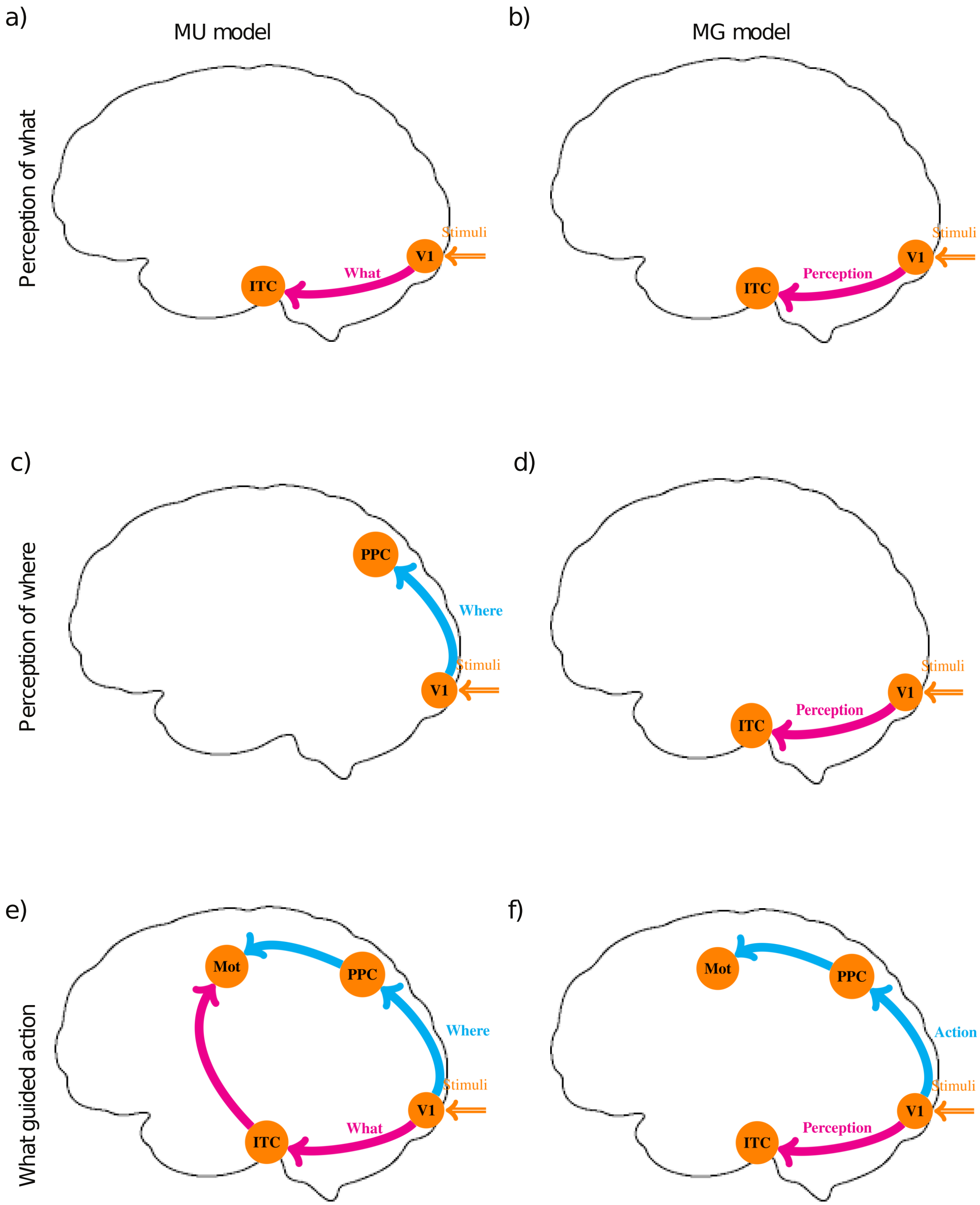



Figure 1

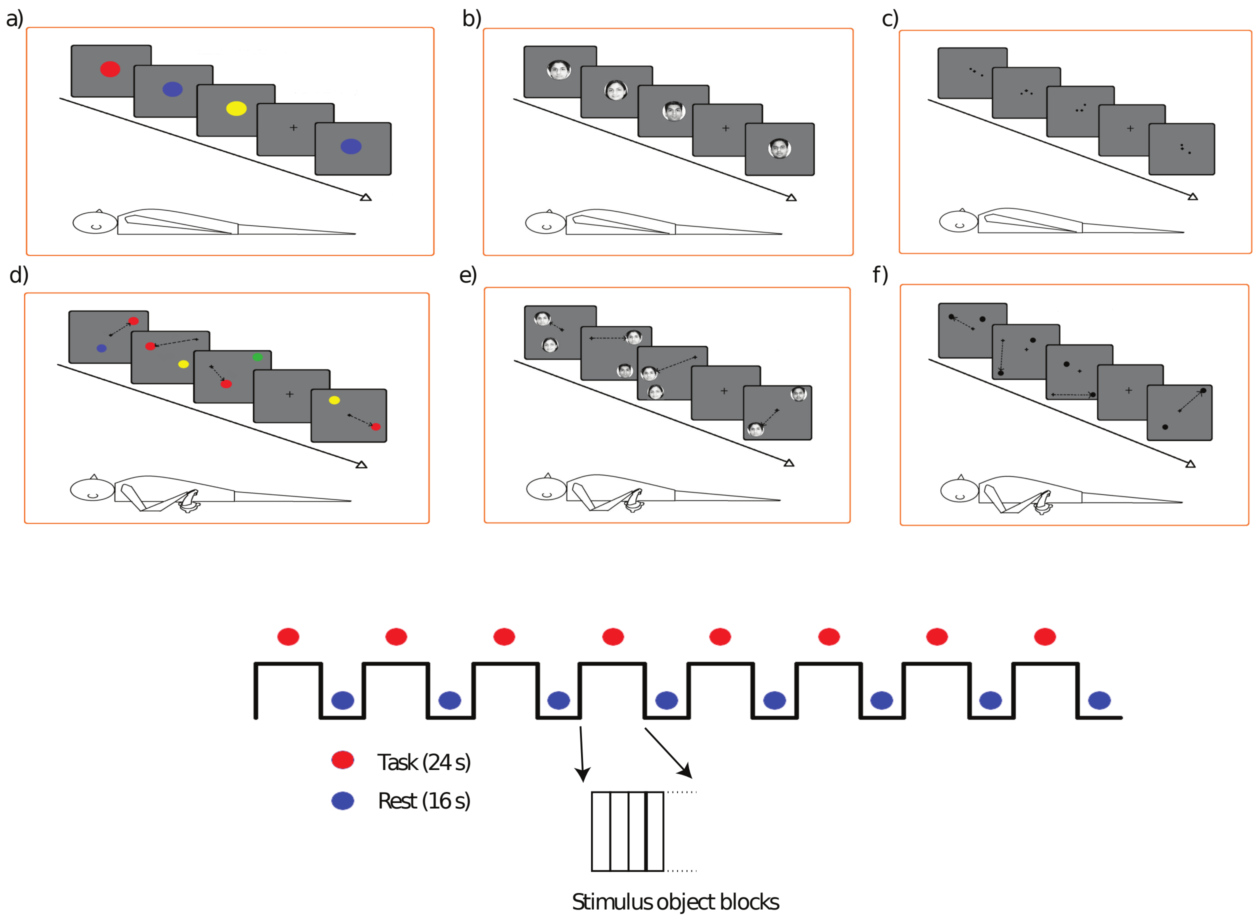
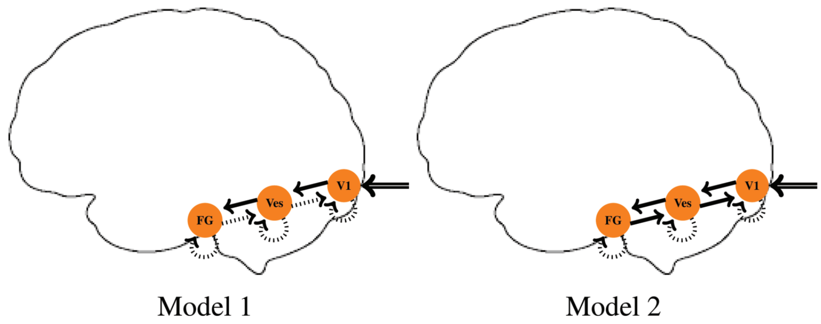
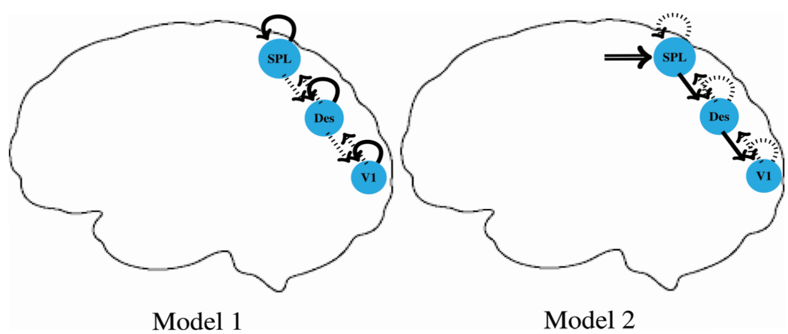



Figure 2

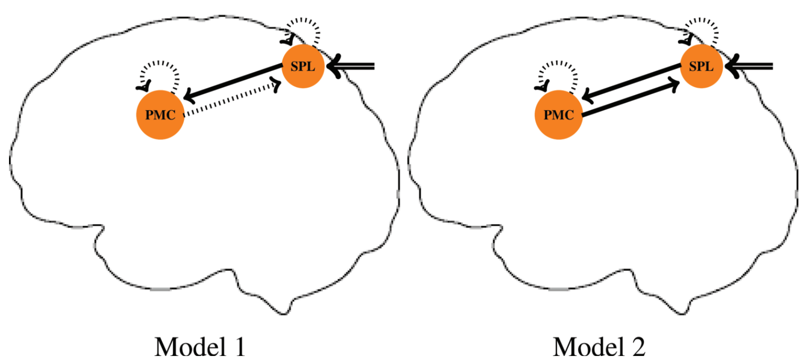
a) Activation model: Color, face perception




b) Deactivtion model: Color, face perception




c) Activation model: Position perception




d) Activation model: Color, face, position action

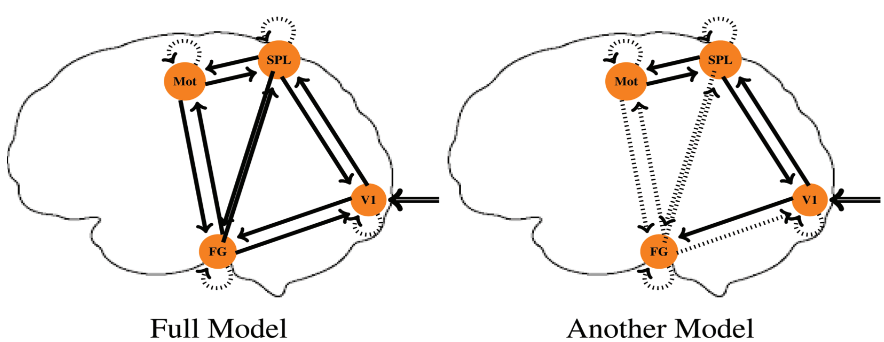



Figure 3

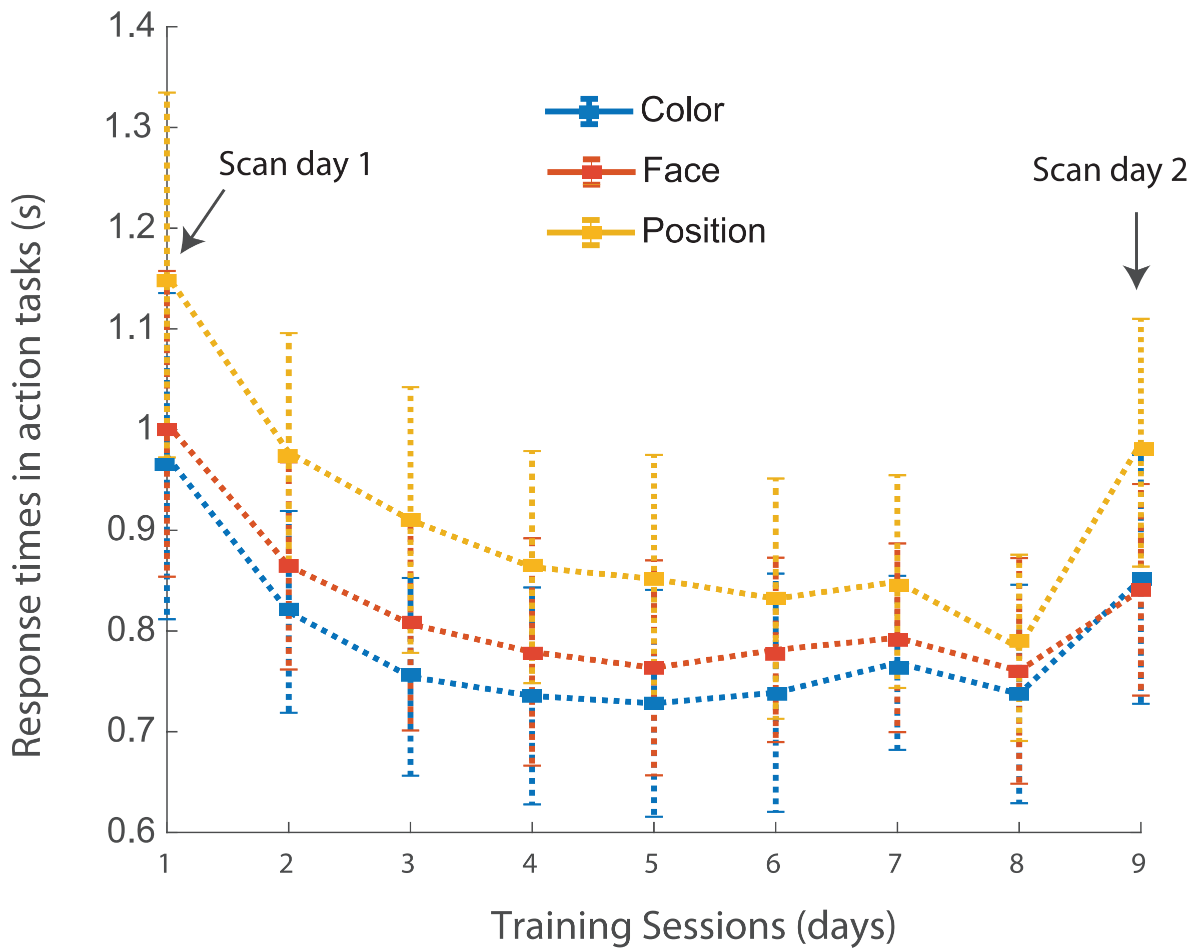

1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
Response times in action tasks (s)
Color
Face
Position
Scan day 1
Scan day 2
1
2
3
4
5
6
7
8
9
Training Sessions (days)

Figure 4

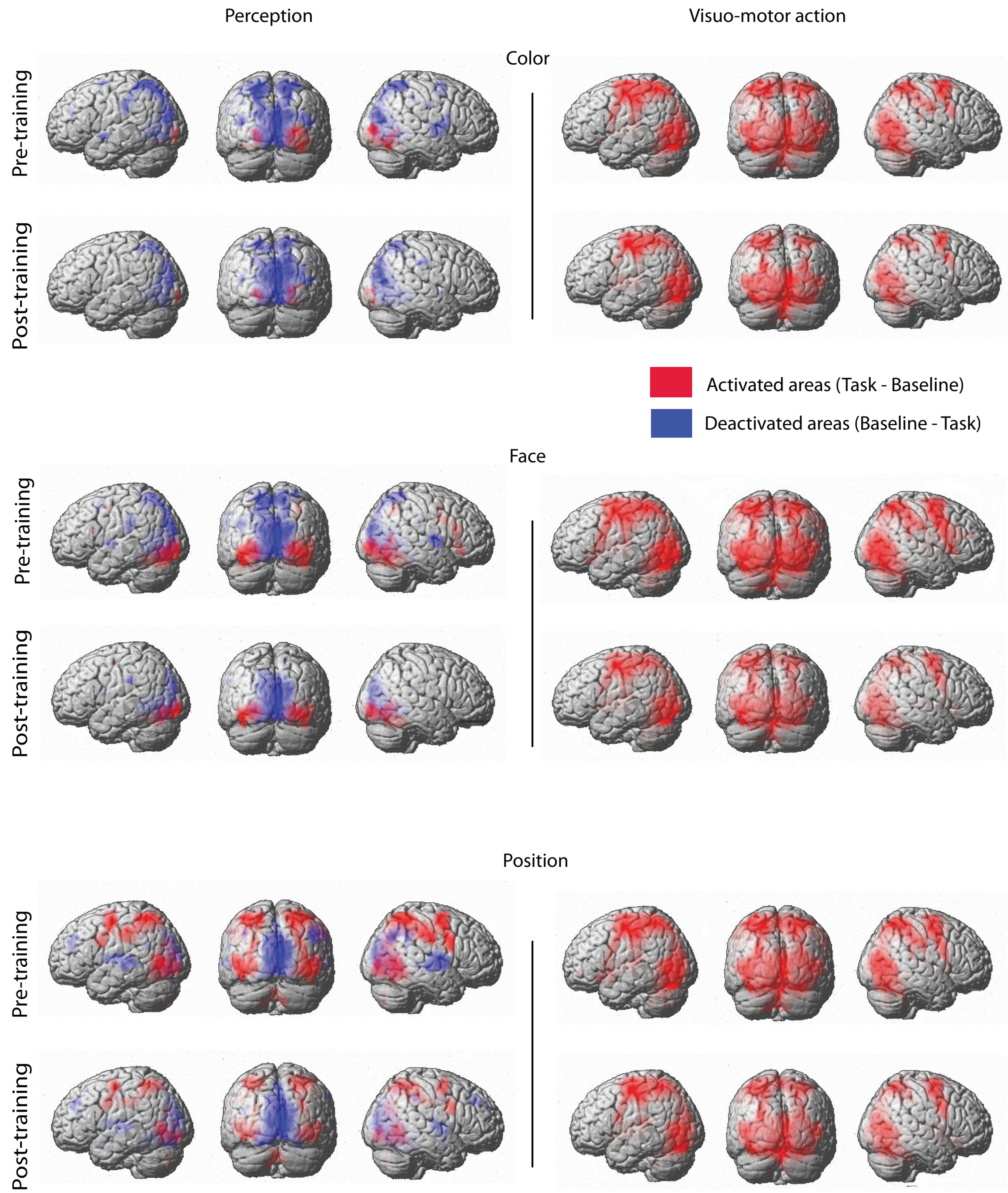
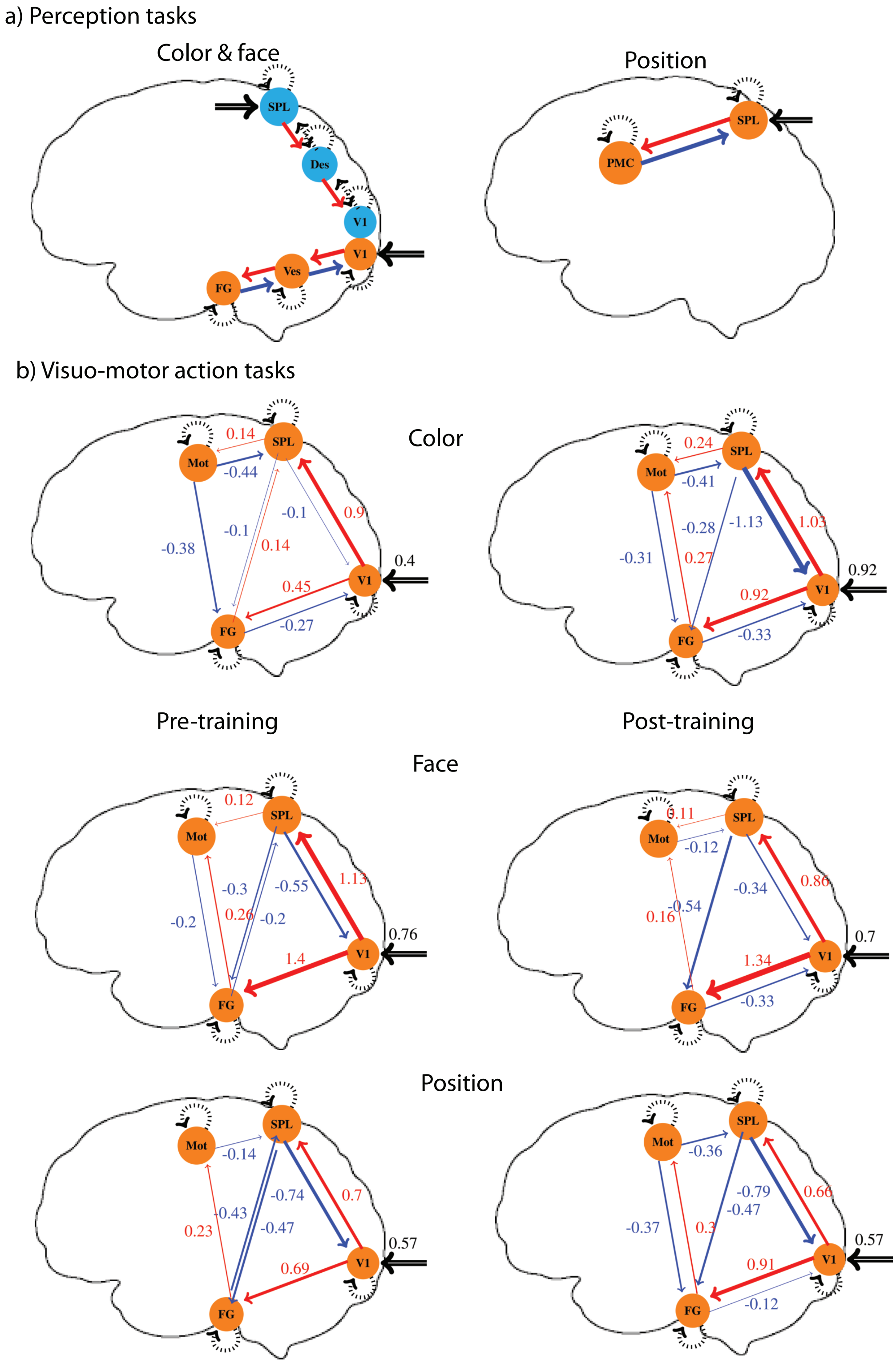

Perception
Visuo-motor action
Color
Pre-training
Post-training
Activated areas (Task - Baseline)
Deactivated areas (Baseline - Task)
Face
Pre-training
Post-training
Position
Pre-training
Post-training

Figure 5



a) Perception tasks
Color & face
Position
SPL
Des
V1
V1
Ves
FG
PMC
SPL
b) Visuo-motor action tasks
Color
Mot
SPL
V1
FG
0.14
-0.44
-0.1
-0.1
0.9
-0.38
0.14
0.4
0.45
-0.27
0.24
-0.41
-0.28
-1.13
1.03
-0.31
0.27
0.92
0.92
-0.33
Pre-training
Post-training
Face
0.12
-0.3
-0.55
1.13
-0.2
0.26
-0.2
0.76
1.4
0.11
-0.12
-0.34
0.86
0.16
-0.54
0.7
1.34
-0.33
Position
-0.14
-0.74
0.7
-0.43
0.23
-0.47
0.57
0.69
-0.36
-0.79
-0.47
0.66
-0.37
0.3
0.57
0.91
-0.12


Figure 6