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Abstract:	This report describes the Month 6 Deliverable for the HBP Subproject 3, Cognitive Architectures. The Deliverable, entitled "Methods, indicators of progress and target values for functional mapping of the human brain and derivation of cognitive architectures selected for cognitive functions," describes SP3's work process and Key Performance Indicators for the ramp-up phase. Based on this report, SP3 will make key contributions to a successful operational phase of the HBP.

Keywords:	Cognitive architectures, strategic experimental protocols, neuro-cognitive constraints, Key Performance Indicators

Document Status

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1. Executive Summary

The Human Brain Project (HBP) Subproject (SP) 3, Cognitive Architectures, will define strategic experimental protocols to dissect associated patterns of brain activation and response dynamics. SP3 will provide protocols to SP2 “Strategic Human Brain Data”. In addition to three actual simulation models (for action recognition, spatial navigation, and multisensory integration), SP3 will provide constraints for the cognitive brain models developed by SP4 “Mathematical and Theoretical Foundations of Brain Research”.

During the ramp-up-phase SP3 is organised into six scientific Work Packages:

1) Perception-Action
2) Motivation, Decision and Reward
3) Learning and Memory
4) Space, Time and Numbers
5) From sensory processing to multimodal perception
6) Capabilities characteristics of the human brain

During the ramp-up phase, SP3 will deliver strategic experimental protocols, generate datasets and provide detailed cognitive architectures. A consistent line-up of milestones and well-defined categorical stage indicators as well as target values have been put up to measure the process and the progress of the scientific work being done. Following the competitive call, the new partners will be fully integrated in the process of work within SP3.

2. Introduction

The Human Brain Project (HBP) is a ten-year research project, funded by the European Commission (EC), with a goal of laying the foundations for a new approach to brain research. The fields of neuroscience, medicine and information technology each have important roles to play in addressing this challenge, but the knowledge and data that each is generating are currently very fragmented. The HBP is driving integration of these different contributions and catalysing a community effort to achieve a new understanding of the brain, new treatments for brain disease and new brain-like computing technologies.

The HBP is based on four divisions: Data, Theory, ICT-platforms and Applications. SP3 Cognitive Architectures belongs to the Data division.

The goal of SP3 is to select well defined, challenging cognitive domains already partially studied by cognitive neuroscience, and to define strategic experimental protocols (previously called "localisers") to dissect associated patterns of brain activation and response dynamics. The observed patterns of activation and dynamics will make it possible to identify a) the brain regions involved in the task, b) the likely circuitry connecting these brain regions, and c) principles of information processing within and between these brain regions. We refer to this information collectively as the cognitive architecture for the task.

SP3 interacts primarily with two other subprojects in HBP:

- SP3 provides protocols to SP2, which will select a subset of them to be run by the Individual Brain Charting task, i.e. a fixed set of human subjects imaged at NeuroSpin (Bertrand Thirion; Task 2.1.1).
- SP3 provides constraints for the cognitive brain models developed by SP4, and three actual simulation models (for action recognition, spatial navigation, and multisensory integration). Models of cognitive architectures will span scales ranging from high-level conceptual models to more explicit models with individual simplified neurons.

2.1 Subproject Structure and Goals

SP3 is led by Stanislas Dehaene (CEA, France). SP3 consists of 7 Work Packages (WP):

1) Perception-Action
2) Motivation, Decision and Reward
3) Learning and Memory
4) Space, Time and Numbers
5) From sensory processing to multimodal perception
6) Capabilities characteristics of the human brain
7) Scientific coordination

We will ultimately deliver cognitive architectures for the HBP Human Brain Atlas (a first version after 18 months, and a second version after 30 months).

- Protocol defined (Month 6): First draft strategic experimental protocols (for functional MRI, MEG, intracranial or electrophysiology) dissecting the brain circuits underlying the corresponding cognitive function and its dynamics and community consensus process initiated

- First datasets (Month 12): Community consensus on those strategic experimental protocols; first datasets generated and protocols validated; first draft cognitive architectures
- Detailed cognitive architecture (Month 18): Detailed cognitive architecture
- Architectures ready for modelling (Month 30): Detailed cognitive architectures transmitted to SP4 for modelling.

3. Methods

In Month 6, WP leaders provided drafts of the following items:

- Strategic experimental protocols. All the WPs generated a first draft protocol for behaviour, functional MRI, MEG, ECOG or other neuroscientific techniques, dissecting the brain circuits underlying the corresponding cognitive function and its dynamics. WP leaders described in a short document the nature of the strategic experimental protocol (previously called "localiser") that they would propose for the cognitive domain under their responsibility. SP2 will ultimately select among those protocols a subset to be run by the Individual Brain Charting task (i.e. a fixed set of human subjects imaged at NeuroSpin). The ultimate goal is to repeatedly scan those subjects until their individual brain networks and their inter-relations are thoroughly understood.
- Synthetic summaries of neuro-cognitive constraints on cognitive architectures. All task leaders are asked to produce "summaries of neuro-cognitive constraints on cognitive architectures". For each domain, 10-20 summary statements of major neurocognitive constraints will be written up. A specific format is being defined for these summaries, and we are working on a first example of a summary statement accompanied by actual data. We currently envisage that each summary statement will comprise the following items:
  - Title of the proposed neurocognitive constraint
  - Short description
  - Quantitative data and benchmarks for modelling (a list of detailed findings)
  - Scientific references
  - Downloadable data sets
  - Relevant theories and models (list of citations or pointers to HBP simulations)
  - Authors
  - Ratings of solidity and replicability (one, two or three stars)
  - Debated issues
  - Search tools (automatic search for related papers in PubMed, GoogleScholar, Frontiers, etc.)
  - Forum for scientists

Each WP leader provided a short list of international experts, inside or outside HBP, who will review the summary statements.

We now describe the specific work packages and tasks proposed by each task leader.

3.1 Perception-Action (WP3.1)

3.1.1 Study of the circuits involved in non-conscious and conscious mechanisms of visual recognition (T3.1.1)

3.1.1.1 Visual Perception

Mapping long and short-term perceptual predictions of the human visual cortex- a combined MEG and fMRI approach (The Malach and Dehaene groups).

3.1.1.1.1 Research goal

The research goal for this task is mapping the spatio-temporal "signature" of long and short-term predictions in the human brain. A major proposal for visual perception is the hypothesis of predictive-coding, according to which the brain constructs an invariant internal model of the object currently being perceived, uses this internal model to send top-down predictions to sensory areas, and uses the "prediction error" (discrepancy between actual and predicted inputs) to revise the internal model appropriately.

The oft-reported phenomenon of "repetition suppression" (reduced visual brain activity when an image is repeated) is consistent with an error signal (under the hypothesis that, *a priori,* the brain expects a stable visual world). Indeed, some paradigms indicate that the reduction in activity in the inferotemporal cortex extends to situations where the animal expects the second image to differ from the first[1].

Invariant visual recognition is thought to rely on the learning of which views are associated with the same object[2], but a review of the theoretical models of this invariant recognition process indicates that the vast majority are feed forward and therefore unable to account for the dynamics of object perception, repetition suppression and error signals.

Rafi Malach (WIS), Stanislas Dehaene (CEA) and Clément Moutard (CEA) have therefore started to review the key existing data, including massive intracranial ECOG data from the Malach lab, that constraint and characterise the temporal dynamics of object recognition and repetition suppression. They will write several synthetic summary statements on this topic. Furthermore, with Ghislaine Dehaene-Lambertz (CEA) from SP2, they have designed a new experiment. If the predictive framework is correct, one will be able to decode, from brain activity, a long-lasting representation of the internal mental model. Error signals will be present if that model does not match reality, whether the expectation is that the image should be repeated or non-repeated.

3.1.1.1.2 Research paradigm

To test this idea and identify the relevant brain systems, the new experiment proposes to record fMRI, MEG and possibly ECOG signals while participants examine an item in slow rotation on screen (either a face or an object, rotating clockwise or counter clockwise at 10 rpm).

We will examine two time scales of prediction: long time scales reflecting the internalisation of natural world statistics, and short time scales reflecting "on-line" acquisition of expectations. In one set of experiments (long term predictions), we will employ natural dynamic changes of an object- e.g. a rotating head or a moving hand. In a second set (short term predictions), different views of a novel object will be learned during an initial exposure period. At certain times, an occluder screen will hide the object

for a variable duration (¼, ½, ¾ or a full turn). When the screen drops, it reveals either the appropriate object or the wrong object, in either the appropriate rotation or the counter-rotation, and with either the appropriate angle or a different angle. If the hypothesis is correct, each of those mismatches should elicit error signals, which fMRI will track in cortical space and MEG and ECOG through time.

Furthermore, decoders will be built to distinguish from brain activity which object is present behind the occluder, and at what angle it is presented. Using the technique of generalisation of temporal decoding[3], we will decipher the temporal unfolding of these internal coding signals and determine how quickly they are revised depending on the (detected or undetected) sensory error. The results will provide strong constraints on the localisation and timing of both internal representation and error detection mechanisms in invariant visual perception. Future work will examine how to generalise these results to the perception of non-conscious (subliminal) views of the items.

3.1.1.1.3 Past data

A crucial aspect in the design of the experiment is the dynamics. We have obtained a substantial amount of past information with regard to signal dynamics in brain response to dynamically changing stimuli—both electrophysiological signals [4, 5] and fMRI [6]. This information will be used to design the present experiments.

3.1.1.1.4 Neuro-cognitive constraints

The main constraint in such a multi-modal experimental approach is to achieve an optimised paradigm that will produce high SNR in both the fMRI and MEG modalities. In the fMRI domain, a major constraint is the slow evolution of the BOLD signal which takes several seconds to develop, although we have previously demonstrated that some information can be gained also at the 1 second resolution[7]. In the MEG domain, the main constraints are poor anatomical resolution of sources (likely within 10 mm resolution) and low SNR. These conflicting constraints will need to be considered when planning the final experimental paradigm. Great care will be invested in experimentally selecting the optimal parameters.

3.1.1.1.5 Timeline for work process

- M6: Optimising the experimental paradigm- psychophysical tests
  - A critical first step in the project is to identify the optimal stimuli and timing of the prediction error experiment. The basic framework involves depiction by human subjects of a motion of an object that disappears behind a screen and then reappears in expected or surprising position or identity. The first six months were dedicated to actually implementing the experiment so that, on the one hand, it could be performed in parallel using MEG and fMRI methodology, and on the other will elicit a vivid sense of surprise. Psychophysical tests conducted outside the MEG and fMRI were carried out to validate the behavioural impact of the stimuli.
- M9: Implementation of the pilot experiments in the MEG facility (Dehaene group) and fMRI (Malach group) - debugging and optimising protocols. The aim is to examine in parallel a number of different stimuli both naturalistic (tool use, sport action, head rotations) and abstract (unfamiliar 3D objects rotation and translation). Importantly, identical experiments will be run on human subjects in fMRI and MEG.
- M12: Data analysis of initial pilot stimuli to validate robustness and reproducibility of brain activations. Selection of main experimental paradigm to be conducted.

- M18: Start of main experimental run on a large cohort of subjects both in MEG and fMRI. An effort will be made to have a subset of subjects running in both the fMRI and MEG modalities.
- M24: Full analysis of the brain imaging results, comparison of MEG and fMRI signals. Particular attention will be made to standardised analysis and modelling that will allow the use of MEG responses as "predictors" of fMRI and vice versa.
- M30: Final analysis and interpretation.

This work will be highly relevant to SP2, since it will provide a central strategic experiment that could be studied longitudinally and across different human populations.

3.1.1.2 Visual attention and the mechanisms of inter-areal communication

3.1.1.2.1 Research goal

In order to behave adaptively in the world, animals are forced to distinguish between relevant and irrelevant sensory information and to select the relevant aspects for further processing. The realisation of this selection process and the reliable routing of selected information require the coordination of neuronal activity in both a top-down (for selection) and bottom-up (for routing) manner across many distributed populations.

A prominent hypothesis for selective inter-areal interactions is communication-through-coherence (CTC), which proposes that information exchange between neural populations is regulated by the degree to which the populations are rhythmically synchronised (Fries, 2005). In vision, attention is thought to select relevant features, locations or objects and to selectively route information from primary visual cortex to higher visual areas in order to facilitate processing. In the case of visual-spatial attention, it has been demonstrated that synchronisation between early and late visual areas occurs selectively between neural populations representing the attended visual stimulus[8,9]. However, a mechanistic account of both the top-down and bottom-up components of this process are lacking.

3.1.1.2.2 Strategic experimental protocols

The lab of Pascal Fries (ESI) has collected several large-scale ECoG data sets from awake, behaving monkeys engaged in a selective attention task. Current and future data being acquired in the lab aim to elucidate how synchronisation is established between distant cortical populations and how synchronisation enhances information transfer between areas. Specifically, we are testing the hypotheses that synchronisation aligns periods of excitability between communicating populations in a flexible manner and that information exchange is selectively enhanced by dynamic gain control between neural populations, i.e. enhancing stimulus-related responses and reducing other sources of variability[10].

We are achieving this by analysis of high channel count, high density, inter-areal recordings of local field potential (LFP) and spiking activity, as well as causal interference and establishment of synchronisation using optogenetics both in anesthetised cats and awake, behaving monkeys. Recordings are increasingly being targeted at the cortical lamina in order to untangle the pattern of intra- and inter-areal synchronisation that is characteristic of information exchange.

3.1.1.2.3 Neuro-cognitive constraints

These data provide critical constraints for models of inter-areal coordination during the execution of learned behaviours. The high temporal resolution and extensive spatial coverage of the recordings allows detailed models of inter-areal interaction to be tested against a large, high quality data set. Ongoing work with the group of Gustavo Deco in SP4

focuses on the dynamic activity of distributed neural populations with respect to systems of coupled oscillators. Using combined laminar arrays with dense recording of surface electrical activity; we will add important information to models of the local field potential and models of extracellular electrical currents from the group of Alain Destexhe (SP4).

Further, our unique datasets are of particular interest to people working on the Neuroinformatics projects of SP5, such as Sonja Grün, because we have large-scale recordings of both spiking activity as well as continuous measurements of the external field. Finally, the large collection of measurements at multiple spatial and temporal scales provides information essential to the construction of detailed large-scale models such as those desired by SP6.

3.1.1.2.4 Timeline for work process

Identifying and analysing circuits for selective information transfer:

- M6: We reviewed models that can account for the selective routing of information between distributed neural populations. We identified all models with a particular focus on differentiating key, empirically testable proposals and constraints in each model. We presented existing data that confirm or refute existing models and note how our current hypothesis, CTC fits into the landscape of existing models and experimental details. Detailed investigation and analysis of circuits for routing and selective information transfer
- M12: We will define strategic data for the evaluation of competing models of selective routing and information transfer. We will have explicit requirements for models of rhythmic synchronisation with respect to putative mechanisms and data that exists to validate these models. We will have requirements for key missing data and experimental protocols to empirically validate or differentiate competing models.
- M18: We will have preliminary analysis of data that elucidate putative mechanisms realising selective routing and information transfer. We will provide a model of intra- and inter-areal communication that can account for empirical observations, as well as make predictions for non-existent strategic data. Specifically, we will evaluate the role of intra- and inter-areal synchronisation with respect to how distributed populations are coupled to achieve selective information transfer.
- M24: We will have a neural model that can implement our phenomenological hypothesis regarding selective routing and information transfer between areas. Our model of laminar based inter-areal interaction will present predictions for the role of local and inter-areal phase synchronisation on dynamic gain control and information transfer.
- M30: We will present key data which impact our model of selective routing and information transfer. We will analyse the effect of local and inter-areal synchronisation on information transfer and storage by applying synchronisation resolved decoding on population activity. We will additionally use optogenetics to causally interfere with local and inter-areal synchronisation based on the predictions of our model of interactions.

3.1.2 Understanding the circuits linking perceptions to actions (T3.1.2)

3.1.2.1 Research goal

The work in the first half-year focused on the neurodynamics of a core circuit of the neural action recognition model developed by Fleischer et al.[11]. This circuit is a nonlinear neural

field that accomplishes the temporal integration information over time, where the input of this structure is provided by neurons, e.g. in the STS, that are selective for form and optic flow patterns[12]. Physiological evidence indicates in addition that many action-selective visual neurons are view-dependent[13], so that such representations likely represent not only the time structure of actions, but also the stimulus view. The dynamic and self-organisation properties of such dynamic neural representations so far have not been studied. The relevant physiological data is from macaque monkeys and was acquired outside the HBP.

Martin Giese (EKUT) and his team proposed a new neurodynamical model for the visual encoding of actions that is based on a two-dimensional neural field. One dimension encodes the temporal structure of the stimuli and the second dimension encodes the stimulus view. The model is based on an Amari field with appropriate lateral interaction kernels specifying asymmetric connections and symmetric competitive interaction in the view direction. In addition, we added a simple linear adaptation mechanism to each neuron.

Through extensive simulation work we could show that this model can reproduce the following effects with relevance for action recognition:

1) Temporal sequence selectivity, as observed in the STS and area F5[14].
2) Bistable perception of biological motion with spontaneous perceptual switching between multiple perceived heading directions from walker silhouettes[15]. The model allows investigating the roles of adaptation and noise in such perceptual switching.
3) Prediction of a bifurcation between a single stable and two competing travelling pulse solutions, dependent on the view angle of the stimulus.
4) The comparison of adaptation for static and dynamic adaptation stimuli provides a possible explanation for the observed lack of adaptation in action-selective neurons[16,17].
5) The adaptation characteristics reproduce the behaviour of neurons in area IT ('input fatigue model')[18].
6) The models predict a new, potentially more effective adaptation stimulus for visual action recognition. In addition, the model is mathematically sufficiently simple to enable a mathematical analysis of the nonlinear dynamics (in progress).

The results of this work have been submitted as abstract to the Computational Neuroscience Conference (CNS) in Quebec and as conference paper to the ICANN 2014 in Hamburg. More detailed comparisons with experimental data are on progress. In addition, we started to collaborate with the Modelling Pillar (Diesmann, Grün) on possible extensions using spiking neuron models, and within the Cognitive Pillar (R. Hari) on exploring a possible relevance of such neurodynamic approaches for MEG.

3.1.2.2 Constraints for cognitive architectures from action recognition derived from a neural model for the recognition of transitive and non-transitive actions

Neural models for action recognition could / should reproduce the following key facts:

- Learning of templates for actions / objects
- Possibility to integrate different types of cues (e.g. form, motion, disparity, and shading cues).

- View-dependence in relevant cortical areas (measured by showing the same action stimuli in different views).
- Sequence selectivity (measured by contrasting stimulus sequences played forwards and backwards); one can see this also as a special form of 'predictive representation', where many Bayesian models in this field are not neurally plausible.
- Sensitivity for the spatial relationship of effector (e.g. hand and goal object; this implies in appropriate areas a lack of responses to 'mimicked actions' where both effector and object are present, but where they do not touch each other in an appropriate way.
- Perceptual multistability (e.g. perceptual switching between different views of different actions).
- Sufficient accuracy to recognise different grip types (e.g. precision or power grip) from monocular videos (without assuming physiologically implausible special mechanisms that provide accurate 3D information).

3.1.2.3 Timeline for work process

- M12: Mathematical analysis of the core neural mass dynamics.
- M18: Comparison with additional data sets from repetition suppression and spontaneous perceptual switching in action recognition.
- M24:
  - Embedding of the extended field in overall architecture.
  - Linking mean-field description to spiking models; evaluating available simulators for implementation of key circuits.
  - Publishing of key results.

3.1.3 Understanding how body perception becomes a reference point for the sense of self (T3.3.3)

This task is led by Olaf Blanke (EPFL) and Mel Slater (UB).

3.1.3.1 Research goal

This work will provide anatomical and functional constraints to SP3 when defining the cognitive architecture of bodily self-consciousness based on human multimodal perception. It will contribute to the definition of a theoretical model of bodily self-consciousness based on Bayesian accounts developed in SP4. Parts of the experimental paradigms developed could be extended to mice models of multimodal perception (SP2; WP5) and will contribute to SP1. Bodily processing and the sense of self will be of relevance for the Neurorobotics Platform (SP10).

3.1.3.2 Strategic experimental paradigms for bodily self-consciousness based on multisensory mechanisms in temporo-parietal cortex

Experimentally controlled changes in bodily self-consciousness will be induced using video and/or virtual reality in combination with robotic devices and MRI[19,20]. Participants will view different images of their body while their body will be stroked simultaneously by the robot with a stick using different forms of synchronous and asynchronous visuo-tactile stimulation, as well as visuo–vestibular stimulation[21,22,23].

Tactile perception[24] and three key aspects of bodily self-consciousness will be measured: self-location, self-identification and first-person perspective. Brain imaging analysis will locally dissect temporo-parietal cortex and also define full-brain functional networks. fMRI (3T; 7T) in these paradigms will define subregions in temporo-parietal cortex (supramarginal gyrus, parietal operculum, posterior superior temporal gyrus, angular gyrus)[25] and be compared with activations induced by unimodal stimulation (tactile, visual, vestibular stimulation) as opposed to activations for distinct body parts (hand, face), and selected cognitive activations (perspective taking, visuo-spatial attention, empathy, theory-of-mind).

Additional analysis using fc fMRI will be used to investigate activation patterns in the same paradigms in IPS[26,27], EBA[28,29], and insula[30,31].

3.1.3.3 Other quantitative data and benchmarks for modelling

- Unique neuro-modelling constraints could be based on additional data (currently not available) in humans using single cell, multi-unit recordings, and local field potentials in humans, awake behaving monkeys, and potentially rodents using comparable multisensory stimulations and behavioural paradigms.
- Self-location, first-person perspective, and self-identification accounts based on Bayesian statistics.

3.1.3.4 Neurocognitive constraints for self-consciousness

- Anatomical constraints (only MRI at this stage).
- Activation of posterior parietal operculum and adjacent parts of supramarginal gyrus during illusory self-location and first-person perspective.
- Illusory self-location and first-person perspective recruit a selective functional network including posterior parietal operculum, supramarginal gyrus and right insula.
- Activation of specific regions in PMC, IPS, and EBA during illusory self-identification.
- Processing constraints (only MRI at this stage).
- Sensory inputs are based on visuo-tactile and visuo-vestibular stimulation.
- Activations should be stroking-dependant.
- Activations should be body-selective.
- Activations should be strongest for trunk stimulation and distinct from activations related to hand stimulation.
- Activations need to be selective with respect to unimodal control tasks.
- Cognitive constraints (only MRI at this stage).
- Activations for self-location are distinct from those of self-identification.
- Activations need to be distinguishable from cognitive activations such as perspective taking, visuo-spatial attention, empathy and theory-of-mind.

3.1.3.5 Timeline for work process

- M6: Ethical approvals.

- M9: Completed review of the strategic data about anatomical and functional constraints in humans and of experimental approaches using robotic stimulation and virtual reality.
- M12:
  - Completed review of the strategic data about anatomical constraints in mice and non-human primates (proprioceptive, visual, tactile integration, in relation with SP1).
  - Anatomical dissection of parietal operculum and inferior parietal cortex (supramarginal and angular gyri) in humans based on existing brain imaging data from the Blanke Laboratory[32,33]. This work is done in collaboration with Simon Eickhoff (from SP2) and will reanalyse fMRI data acquired at 3T.
  - Functional dissection of the areas mentioned above, check for co-activations with cognitive functions (perspective taking, visuo-spatial attention, empathy, theory-of-mind) based on meta-analysis. This work is done in collaboration with Simon Eickhoff (from SP2).
- Experimental design for main experiment finalised.
- M15: Start of the main experimental study on bodily self-consciousness, also using selected unimodal and cognitive control functions.
- M24: Finish of the main experimental study.

3.2 Motivation, Decision and Reward (WP3.2)

3.2.1 Mapping and understanding the neuronal circuits involved in decision making, confidence and error correction (T3.2.1)

The group has progressed in defining experimental protocols to measure confidence in decision-making that have the following requirements:

- Can be adapted to different animal models (humans, monkeys and rodents).
- Can be adapted to different stages of development from infants to adults.
- Express general attributes of confidence that are not modality or domain specific.
- Are amenable to be represented by simple models of decision-making.
- Allow confidence judgments to be decorrelated from decision signal and other variables of the decision process. This is a requirement for fMRI and MEG, to use the confidence signal as an independent regressor in a linear model or classifier.
- Allow different attributes of confidence (criterion, biases, accuracy, properties of the distribution) to be measured independently.

The Paris (Stanislas Dehaene, CEA), Lisbon (Zach Mainen and Rui Costa, FCHAMP) and Buenos Aires (Mariano Sigman) groups have worked in concert in the development of a set of tasks that achieve these requirements. In these six months, we achieved the following:

- Demonstrated that implicit measures of confidence (such as waiting time) which are the only resource to inquire about confidence in animal models and in young children correlate tightly in a subject by subject basis with explicit measures of confidence.

- Showed that while different measures of confidence correlate, each has their own idiosyncrasy (for instance, wager is shifted towards lower values of confidence due to risk aversion policies). This research has constrained and optimised the different possibilities to acquire confidence judgments.
- Showed that some aspects of confidence distribution (such as the bias towards over and under confidence) are extremely replicable across tasks and sessions. Other aspects such as the precision of the confidence system are more variable across tasks. This dependence is more related to task structure (number of options, type of decision) than to modality (visual, auditory).
- Demonstrated that several models of confidence (based on Ideal Bayesian Observers, Signal Detection Theory, or even neuronal architecture descriptions) are capable of explaining data of choice, response time and confidence. The models provide hidden variables that are not observable by direct inspection which serve as regressors in the neuroimaging experiments.
- Demonstrated that in regular sequences in volatile conditions (where probabilities of the underlying generating processes change abruptly) subjects can efficiently and rapidly detect these changes. Subjects make very accurate predictions of the probability of an event and can report switching between models. The confidence estimates are partly decoupled from external probabilities and can be explained by second order models (how much a subject trusts a model and how much the model trusts the prediction).

3.2.1.1 Strategic experimental protocols

Based on these series of experiments done in children, adults, mice, and with different ways of measuring and conveying confidence, the group converged on a candidate experimental protocol to measure computations of confidence and of probability distributions (of external events and trust and beliefs in our own actions). The first round of experiments will be done only in adults using fMRI and MEG to combine fine spatial and temporal resolution.

The protocol is based on a rapid (about 1 Hertz) sequence of binary events. Sequences are defined in segments by stochastic processes with a given distribution. The generating process shifts abruptly generating situations of volatility (where uncertainty is unknown) after which subjects can learn and consolidate a new probabilistic model. Sequences are presented in different sensory modalities to identify amodal components of the constructions of probabilities. Subjects report whenever they think probabilities have changed, in which case they report how far in advance they began to foresee that they had to change the model. In a small fraction of trials (but sufficient to generate reliable statistics in one experimental session), participants provide their prediction in a continuous scale (the degree of trust of an outcome by the model) and their confidence in the choice they have made. The paradigm should identify the updating process of a model, the loss of trust (lack of confidence) in a given model, and how this is abruptly changed by re-setting to a new model that is shifting to a new progressive rise in confidence. An important feature of the protocol is that it can distinguish estimates of external probabilities (prediction) from confidence.

3.2.1.2 Timeline for work process

- M6: The group defined, based on review of the data and behavioural pilots, two experimental protocols to measure computations of confidence and of probability distributions.

- M12: We will have collected data for the first MEG and fMRI experiment of the dynamics of confidence and probability distributions (Experiment 1). At 12 months, we will also begin a rodent version of Experiment 1 where confidence is expressed by implicit markers such as waiting time, opting out frequency (Experiment 2).
- M18: Experiment 1 will be fully analysed and we will start collecting data for Experiment 2. Experiment 2 will be done in collaboration with SP2 as part of massive fMRI data acquisition. We will investigate decision-making, followed by confidence between domains with very precise localisation in the fMRI signal (places and faces). Details of the experiment will be piloted during the first 18 months. This experiment will distinguish whether confidence computations are performed in the same cortical circuits that compute the decision signal or rather by a specialised network.
- M24: All experiments (humans and rodents) will be fully analysed. These experiments will provide constraints both at the large scale of functional networks (from fMRI experiments) with fine timing resolution (MEG Experiment 1) and with details of cortical circuits implementing the confidence signal (experiments in rodents). The group will join efforts with the theory groups to define first to low-dimensional models of decision making and then to full brain models at the neuronal level of decision making.
- M30: We will provide neural-level simulations of agents capable of constructing beliefs of confidence in decision-making revealing human like behaviour.

3.2.2 Mapping and understanding the neuronal circuits involved in motivation, emotion and reward (T3.2.2)

This task is currently not funded and will start at Month 13. It is led by Mathias Pessiglione (ICM).

3.2.2.1 Research goal

The general objective is to build a neuro-computational model of the mechanisms that motivate the behaviour. These mechanisms include:

- Assigning subjective values to potential world states
- Comparing values so as to select the best option
- Aligning the direction and intensity of behaviour to the selected goal
- Updating option values based on the experience of behavioural outcomes

To probe the neural correlates of these basic mechanisms, a set of short behavioural tests will be developed. The idea is not to imagine new tests but to optimise existing tests in order to target key dimensions of motivation. These tests will be used in:

- Neuroimaging studies – We will employ both fMRI in healthy subjects and intra-cranial recordings in epileptic patients to characterise the spatio-temporal pattern of activity underlying motivational processes.
- Clinical studies – Patients with neurological or psychiatric conditions will perform the same tests to establish causal links between neural perturbation due to disease or treatment and behavioural deficits.

Results will be communicated in the form of review papers. These papers should:

- Position a particular test with regard to the relevant literature

- Suggest a computational account of the targeted mechanisms
- Provide links from computational variables and processes to neural entities

In the end, the neuro-computational models developed in this task should enable predicting behavioural disorders from simulated neural perturbations, and reciprocally, inferring neural dysfunction from observed behavioural deficits.

3.2.2.2 Timeline for work process

- M18: Definition of the architectural question completed. Battery of behavioural tests designed and programmed. Pilot fMRI data acquired. Testing of patients with motivational deficits (prefrontal vascular lesions, fronto-temporal dementia, major depression episode, schizophrenia with negative symptoms) started.
- M24: FMRI data acquired in 24 healthy subjects. FMRI data analysis started.
- M30: Behavioural data acquired in around 24 patients per clinical condition. Data analysis completed. Drafts of review papers including computational modelling produced. List of neurocognitive constraints of architectures underlying motivation constructed.

3.3 Learning and Memory (WP3.3)

3.3.1 Skills and habits (T3.3.1)

Procedural memory: Protocol for imaging repetition dependent brain activity modulation as brain signatures of motor skill consolidation in young healthy human adults.

3.3.1.1 Research goal

The aim of the studies is to address cortical dynamics (repetition suppression, repetition enhancement, functional connectivity) as brain signatures of accumulating experience, plasticity and procedural memory consolidation in motor skill learning in typical young adults. The strategic experimental protocol for functional MRI of procedural memory involves using cortical dynamics as signatures for repeated experience, learning and memory consolidation

A key strategic point is that Avi Karni's group (UHAIFA) is following the work of Karni et al.[34,35] by looking at short term modulations of the evoked BOLD signals in motor cortex and the motor system in general as enduring signatures of previous experience, and importantly, as signatures of overnight procedural memory consolidation. Therefore, we are testing the conjecture that activity in a given brain area is modulated by task repetition as a function of whether prior experience was afforded. Complementing this focus on the temporal modulation of activity (as reflected in the metabolic BOLD signal), we are also testing for repetition dependent modulations of the functional connectivity between areas engaged in the performance of the task.

The basic study protocol is the following:

- On day 1, all participants are instructed (full declarative knowledge) and shown a specific sequence composed of 5 opposition movements, identical to the sequences used by Karni et al. [36] and Korman et al.[37,38] . Performance tests (speed, accuracy; video analysis) are performed before and after a structured training session that has been shown to trigger the expression of significant delayed gains in performance, overnight, in the majority of participants.

- On day 2, participants are scanned during the paced performance of either the movement sequence intensively trained a day earlier, or a similarly constructed, but novel, untrained sequence. Both movement sequences are performed in pairs of blocks separated by a brief rest interval (30 sec). The scanning session is followed by a third performance test to assess the expression of delayed "offline" gains.

Functional magnetic resonance imaging scanning is carried out using a 3 Tesla whole body high definition system (GE EXCITE 3 HD) equipped with an 8-channel head coil. Pre-processing and statistical analysis of the data are carried out with Statistical Parametric Mapping (SPM8) (Wellcome Department of Cognitive Neurology, London, UK) operating under Matlab R2012a (The Mathworks Inc., Natick, MA, USA). Statistical analyses of BOLD signal changes are performed using a general linear model (GLM)[39]. ROIs are defined in each individual brain using a combined anatomical and functional approach. Raw ROI time-courses are extracted from pre-processed functional images for each run using the MarsBar toolbox for SPM[40]. These raw BOLD signals are converted to percent signal change. A seed-driven approach is applied to explore changes in functional connectivity during FOS performance. Individual ROIs within M1 were used as a seed. Connectivity analyses, on pre-processed functional images are run using the Functional Connectivity Toolbox (Conn) for SPM[41].

In Experiment 1, brain activation induced by actual performance is studied. In Experiment 2 we plan to compare brain activations and repetition effects evoked by actual performance to activation evoked by movement observation of the identical movement sequences to explore motor learning and memory consolidation by action observation.

3.3.1.2 Neurocognitive constraints

- Triggering of procedural memory processes – consolidation processes can be triggered in a given training experience only if a minimal number of task repetitions (task iterations) are afforded.
- Saturation of repetition priming (adaptation) effects – consolidation processes can be triggered when practice has resulted in within session performance stabilisation (training to plateau) reflecting a saturation of adaptation, task specific tuning, and processes.
- Specificity – consolidation processes lead to trained task conditions specific procedural knowledge, reflecting the tuning properties of the local neuronal populations undergoing plasticity.
- Systems level consolidation – different neuronal populations are involved in representing the acquired skill at different levels of experience (thus, changing profiles of specificity).
- Gating - consolidation processes are gated by the (behavioural) relevance of the task as well as by reward.
- Interference – within a time window of a few hours the mnemonic process can be halted by conflicting experience (presumably reflecting neuronal level overlap between the two tasks).
- Maturation/age effects – the time window for interference is extended in maturation (puberty).
- Sleep dependency – time in sleep is necessary for the expression of delayed consolidation phase gains (presumably, stage 2 sleep, spindles). Time in sleep can

condense and shorten the time constants of procedural memory consolidation processes.

- Action observation vs. actual performance – although observation of movement can be effective in driving learning and triggering procedural memory consolidation it may lead to plasticity at neuronal populations different from those involved in skill acquisition by actual practice.

3.3.1.3 Timeline for work process

Experiment 1: Brain signatures of motor skill consolidation in young healthy human adults (fMRI study)

- M6: Analyses of pilot runs (past data)
- M18: Acquisition of full data set
- M24: Write-up and submission

Experiment 2: Differential effects of observation and actual movement performance on procedural memory consolidation (fMRI study, Behaviour)

- M6: Analysis of behavioural data (past data), experimental design and programming of fMRI study
- M12: Write up of behavioural data (past data), analysis of fMRI pilot runs
- M18: Acquisition of full fMRI data set
- M24: Analysis of full fMRI data set, write-up

3.3.2 Memory for facts and events (T3.3.2)

3.3.2.1 Episodic Memory: Protocol for spatiotemporal dissociation of human hippocampus computational modes in encoding and retrieval of single events.

Understanding the role of the hippocampal formation in memory operations is essential for brain simulation. Some of the basic issues are yet unknown and require binding of experimental data, computational approaches and simulations. A key strategic point is related to the model-based posit that the hippocampus operates in two mnemonic-related basic computational modes: pattern separation in encoding and a pattern completion in retrieval. Yet, the modes alternate in each phase in which they operate conjointly. Identifying the activity signatures and kinetics of this alternation in hippocampal subregions and how is it affects output is critical for constraining realistic simulation.

Yadin Dudai's group developed in the laboratory a protocol type to address the above goal in the human brain, based on their finding that the hippocampus responds differently to the onset and offset of realistic episodic stimuli and toward novel and familiar stimuli. It is composed of a Study phase in an fMRI scanner (divided to runs on Day1,2), and a Test phase (Day2). During Study participants are presented with brief narrative movie clips (8s) previously unfamiliar to them, interleaved with "rest"—fixation screens of variable duration (8-16s). The clips are divided randomly into Repeated (6 times across Study) and Non-Repeated (presented once). On Day1, all Repeated clips are presented 4 times, across 4 runs. On Day2, the first run serves as a reminder run, in which all Repeated clips are presented (5^{th} presentation). During the following 2 runs, all clips (Non-Repeated and repetition 6 of Repeated) are presented in random order. The Test, outside the scanner, consists of computerised cued-recall gist test and confidence rating.

Functional imaging is performed on a 3T Trio Magnetom Siemens scanner using standard procedures [42]. Data are pre-processed and analysed using BrainVoyager QX 2.4 in combination with in-house code incorporating the Neuroimaging Informatics Technology Initiative (NIfTI) toolbox and NeuroElf (V0.9c). Probabilistic independent component analysis is run using the Multivariate Exploratory Linear Optimised Decomposition into Independent Components tool of the FMRIB Software Library v5.0. Anatomical hippocampal ROIs are defined for each participant, projected into each participant's ACPC-space and corrected. Hippocampal ROIs are segmented to anterior/posterior (AP) sections at the first coronal slice in which the uncal apex is visible. Average time-course for each ROI is normalised (z-score) and used for calculation of ROI-based GLM analyses.

3.3.3 Working memory (T3.3.3)

3.3.3.1 Research goal

Working memory (WM) maintains information over brief periods of time. This feature is required for goal-directed behaviour and allows us to act beyond the confines of the here and now. WM can thus be conceptualised as providing an interface between perception, long-term memory, and action. As such, WM is taxed by numerous laboratory- and everyday cognitive challenges. Previous human and primate research has shown that WM is implemented by a network of brain regions, but the specific contribution of each network component remains unclear. In particular, it is unknown how the characteristic limited capacity of WM results from the functioning of different part(s)/network interactions.

T3.3.3 will contribute to the theoretical model of working memory developed by T4.3.2 ("models of working memory and the effects of attention").

3.3.3.2 Strategic experimental protocol for functional MRI of working memory: Delayed match-to-sample

Working memory (WM) is a fundamental capacity that is taxed by numerous laboratory- and everyday cognitive challenges. Here Lars Nyberg's group (UMU) proposes a delayed match-to-sample (DMS) protocol that captures the essence of WM: maintenance of information during a delay period when there is no sensory input/external support (Figure 1). Various versions of the DMS task have been used in many past human and primate studies, and many neurocognitive constraints have been identified.

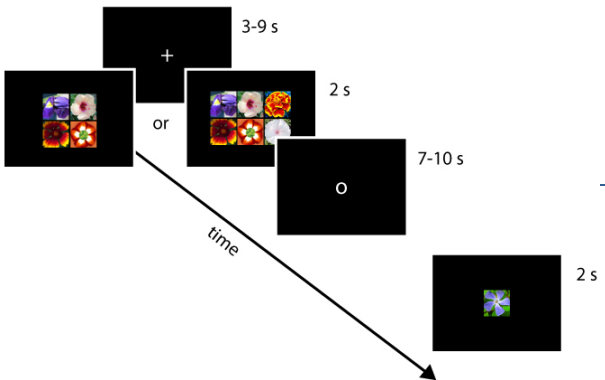

Figure 1: Overview of the protocol

The different trials in the protocol are interspersed by 3-9 sec long ITIs (fixations). 1) Each trial starts by presenting a set of visual stimuli (4-6 flowers) and the participant is instructed to memorise these stimuli. 2) Then follows a delay period when the participant holds the visual information in WM for 7-10 s. 3) Lastly, the test phase consist of a match-to-sample task ("does the presented stimulus match any flower in the sample"; Yes or No?).

The proposed protocol enables identification of brain regions that interact during temporary maintenance of information in WM, notably frontal and posterior cortical regions. In a pilot experiment we used 20 items of each load (in that case, 2-4 stimuli). At the individual as well as group level (18 participants), the protocol robustly elicited increased fMRI BOLD signal in several brain regions at each of the phases of the DMS task (memorisation, delay, test). Importantly, as predicted, sustained effects in fronto-temporal regions were observed during the maintenance phase (Figure 2), which is consistent with several past studies.

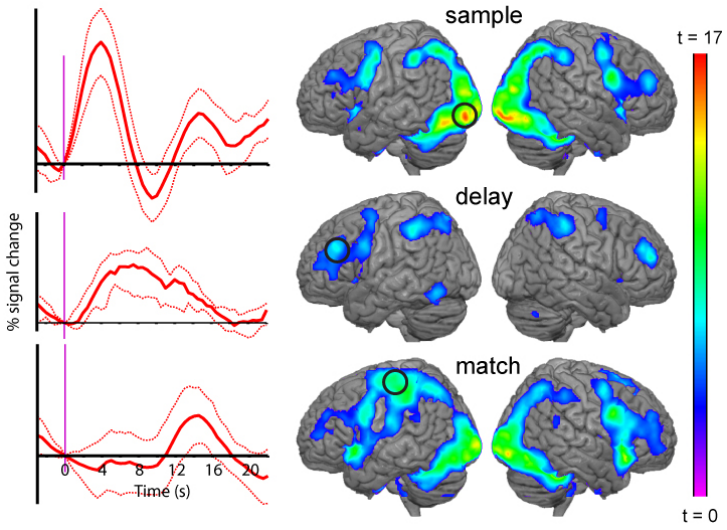

Figure 2: BOLD signal change for the different trial phases

With the time parameters as in Figure 1, an experiment with 40 items takes about 13 minutes, and 30 trials will fit in 10 minutes. Should more time be allowed, possible extensions involve acquiring data on both correct and incorrect responses, and/or varying the number of items in the stimulus set so as to vary the WM load.

3.3.3.3 Neurocognitive constraints

- Accessibility – The representations held in working memory are accessible for use in relation to other processes, such as planning, decision-making, etc., providing an interface between perception, long-term memory, and action.
- Durability – The representations held in working memory last for several seconds to minutes without external support. Durability relies on active processes such as rehearsal ("refreshing" the content), without which the representations decay within a few seconds.
- Capacity limitations – Working-memory capacity is limited and may only contain 1-4 items (absolute limits remain controversial). Capacity can be increased through "chunking" bits of information into more complex units.
- Modularity – Working memory is not a unitary process, but results from the interaction between several relatively separable modules. Key modules (highly schematic) are a) item-representation modules that temporarily stores working-memory content, and b) attention/executive modules that control the content of working memory through processes such as selection and updating, interference resolution, etc.
- Manipulability – The content of working memory can be manipulated such that the content itself can be "worked on" and changed, e.g., during mental arithmetic.
- Distraction/interference – Working memory processes are sensitive to interference, which is a major factor for working-memory failure.
- Input – The content of working memory can come from several different sources, e.g., visual or auditory sensory, but also from long-term memory.
- Brain regions – Several different brain regions contribute to working memory, reflecting its modular nature.
- Prefrontal cortex – Persistent neural activity during working memory has been demonstrated consistently and is likely to reflect goal-related, cognitive control representations, although traditional interpretations suggest that PFC activity reflects working-memory content.
- Parietal cortex – Attention and spatial representations.
- Sensory cortex – Recent research suggest that working-memory content is represented by activity in sensory regions; the specific region depends on the specific content.
- Basal ganglia – Suggested important for updating working-memory content.
- Cerebellum – Mainly implicated for verbal working memory, but also for other forms.

3.3.3.4 Timeline for work process

In addition to the strategic protocol, we plan to perform a protocol locally that explicitly addresses WM capacity limitations.

- M12: Preparations, programming, and pilot runs.
- M18: Full data set and analyses.
- M24: Write-up and submission.

3.4 Space, Time and Numbers (WP3.4)

3.4.1 Identifying and analysing the multi-modal circuits for spatial navigation and spatial memory (T3.4.1)

3.4.1.1 Research goal

This work will contribute to the definition of the theoretical and computational models of rat behaviour in navigation tasks that will be one of the principal interests of SP3 and SP4. The modelling work will be in part suitable for implementation on the large-scale network models developed in SP6, and in the neuromorphic computing devices implemented in SP9.

3.4.1.2 Neuro-cognitive constraints for models of spatial navigation

HBP-funded work has focused on defining the minimal set of experimental results that should be explained by an initial model of spatial navigation. This includes the basic spatial firing properties of place cells, head direction cells, grid cells and boundary cells (e.g. reviewed in Hartley et al.[43]), and the basic effects of lesions or inactivation to hippocampus and striatum, summarised by the experiments described by Pearce et al.[44], Packard and McGaugh[45], and Doeller et al.[46]). In these experiments, an agent (rat or person) can move inside an area (a water maze or 'plus' maze for rodents, left and right panels, Figure 3), or a virtual environment for humans (middle panel, figure 3), including distance visual cues for orientation, environmental boundaries and possibly an intra-maze landmark. The task is to learn the location of a hidden platform (rodents) or of several objects (humans) relative to the various environmental cues, and also self-motion-related information (aka "path integration") if a consistent path is used. The hippocampal formation is implicated in learning locations relative to environmental structure, oriented by distant visual cues, and appears to use an incidental learning rule; while the striatum is implicated in learning locations relative to intra maze landmarks and path information, also oriented by distant visual cues, and appears to use a reinforcement learning rule.

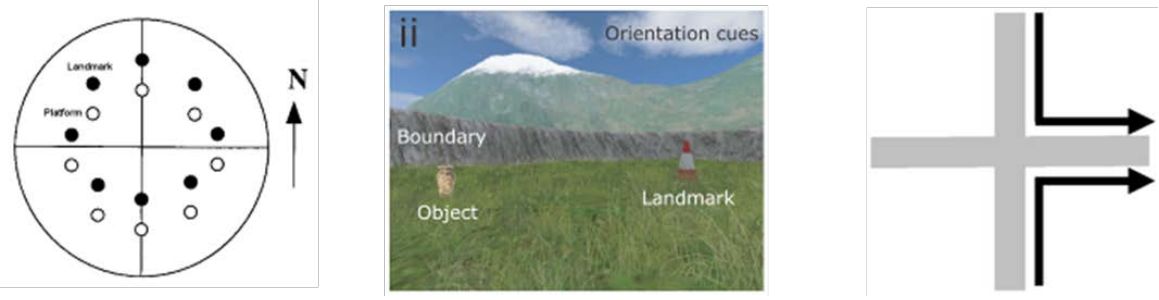

Figure 3: Behavioural tasks assessing spatial navigation.

Left: A variant of the Morris water maze for rodents, in which an intra-maze landmark indicates the location of the hidden platform, in conjunction with the boundary of the maze and distant visual cues for orientation. The landmark and platform can move together between trials (8 locations shown[47]). Middle: An analogous virtual environment for testing human spatial naviagtion[48]. Right: A 'plus' maze, in which rodents learn a reward location from one start arm (e.g. the East arm, starting from the South arm) and occasionally start from the opposing (North) arm to test for use of a body-turn or allocentric representation of the goal location[49].

3.4.1.3 Strategic experimental protocols

The virtual environment object-location task (Figure 3, middle) has been verified to successfully indicate several aspects of human spatial navigation. Learning object locations

relative to the boundary activates the hippocampal formation, while learning them relative to the landmark activates the dorsal striatum[50]. This involves incidental and reinforcement learning rules respectively[51], and induces theta rhythmicity in medial temporal and medial prefrontal regions[52,53].

3.4.1.4 Modelling the neural bases of spatial navigation

In collaboration with projects supported by UK funds, Neil Burgess' group (UCL) has reviewed current models of self-location during navigation, focusing on the neural mechanisms underlying the firing of place cells, head direction cells and grid cells[54]. The reviewed evidence relating to the functional contribution grid cell firing makes to place cell firing[55] and produced a 'hybrid' model of grid cell firing based on continuous attractor dynamics and theta-band oscillatory interference[56].

HBP-funded work has focused on planning a biologically realistic computational model of the hippocampal-striatal circuit that is engaged during navigation tasks[57,58,59]. The final aim of such a model would be to follow the neuro-cognitive constraints listed above, including neural-level simulation of the interaction between hippocampal and striatal systems in controlling navigation[60].

3.4.1.5 Timeline for work process

Identifying and analysing multi-modal circuits for spatial navigation:

- M6: We reviewed models that integrate sensory and self-motion information in self-localisation, mediated by place and grid cell firing in the hippocampal formation.

Models of spatial navigation

- M12: We will have a defined the strategic data for modelling hippocampal navigation, based on existing literature, and have started on simulating data regarding the hippocampal-striatal circuits for self-localisation and goal-directed navigation.
- M18: We will have preliminary data on a small-scale, firing rate coded, network model of hippocampal navigation: combining sensory inputs, path integration, and attractor and oscillatory dynamics, including the firing of head-direction, place and grid cells.
- M24: We will provide initial results on simulations of hippocampal based navigation, and pilot data regarding simulation of striatal navigation.
- M30: We will provide neural-level simulations of agents (rats or humans) performing well-known experiments such as the water maze or the virtual arena. These simulations should be comparable to *in-vivo* electrophysiology (firing rate data) and with behaviour, including the effects of inactivation of hippocampal or striatal systems on behaviour.

3.5 From sensory processing to multimodal perception (WP3.5)

The tasks covered in WP3.5 are led by Yves Frégnac (UNIC-CNRS, WP3.5 leader) and Brice Bathellier (UNIC-CNRS) and implemented at the UNIC CNRS research centre. Models in the second phase of the project will be developed in collaboration with Andrew Davison (UNIC-CNRS).

The task goals are to provide observations to constrain models of primary sensory cortical area aiming at reproducing the neural correlates of low-level perception in a unimodal

(T3.5.1) or multimodal (T3.5.2) context. The integration strategy used here proceeds in several incremental steps. The first step is to extract, from existing data, generic principles that will define a first set of modelling constraints. This, in turn, will lead to the definition of strategic experimental paradigms. Their implementation will lead to novel data that will be used to test the validity of the coherence in knowledge integration obtained in the proposed models.

3.5.1 Neural correlates of unimodal perception and self-organisation of internal knowledge in mammalian primary cortical areas (T3.5.1)

3.5.1.1 Neuro-cognitive constraints of interest

The goals here are:

1) To identify the circuits and main connection types involved in low-level perception in the early visual system of higher mammals.
2) To refine our knowledge of canonical circuits and their computational roles.
3) To build realistic data-driven models that accurately account for the emergence of low-level rules in the human Brain, allowing binding of information from the sensory periphery (Gestalt theory).

3.5.1.2 Strategy

The project proceeds in two steps corresponding to the two phases of HBP:

- 1st phase (Ramp-up 0-30 months): identifying protocols and computations performed by early sensory cortical areas, with an emphasis on the visual system as a reference study, and providing a theoretical framework for the integration of multisensory interactions in population representations of sensory stimuli.
- 2nd phase: Construct a strategic set of multiscale observations in the mammalian brain (rodent and cat) in order to constrain a realistic model of low-level perception and multimodal integration. A collaborative work will be done with the Simulation and Theory SPs to implement cognitive architectures into cognitive models, first focusing on principles of sensory coding extracted from invasive multiscale studies, before proposing a theoretical framework for multimodal integration and sense merging.

3.5.1.3 Protocols

In the first six months, unified parametric protocols were proposed to search for the stimulus dependency of the temporal precision and sparseness of the neural code, for stimuli ranging from gratings to dense noise, including animated natural scenes with realistic eye-movements. The data obtained earlier with intracellular techniques have been processed and published. The same exact protocols are now applied to study the evoked dynamics with mesoscopic measurements (local field potentials (LFP)s, multiple simultaneous recordings (MUA), and voltage sensitive dye (VSD) when possible).

3.5.1.4 Strategic data

- The intracellular data from anesthetised cat visual area V1 demonstrates the dependency of the neural code on the input statistics. They support the view that the sparsening and the time precision of the neural code in V1 may depend primarily on three constraining principles:
  - The spike timing precision of the code depends of the broadbandness of the input spectrum: using realistic simulation of oculomotor exploration of natural scenes,

the input bandwidth is shown to be rich enough for recruiting optimally the diversity of spatial and time constants during recurrent processing.

- The spike timing precision is conditioned by the temporal interplay of excitation and inhibition: *in vivo* voltage clamp and current clamp estimates of conductance measurements demonstrate that natural scene statistics narrow selectively the duration of the spiking opportunity window during which the balance between excitation and inhibition changes transiently and reversibly.
- The sparseness/denseness of the spiking regime is conditioned by the subthreshold membrane potential in the lower frequency band: a minimal level of power is needed below 10 Hz to reach consistently the spiking threshold. This situation results in sparse activity in (non-optimal) natural scene processing, whereas the spiking threshold is rarely reached with visual dense noise.

3.5.1.5 Models

These data are currently used to build a comprehensive data-driven model of V1 in the higher mammals (cat, ferret, monkey) applicable to man. A first approach has been developed by two European labs outside HBP: the Institut de Neuroscience de la Timone (INT), and the Freiburg Bernstein Center in partnership with the lab of Jose Manuel Alonso (SUNY, USA). The model incorporates the CNRS-UNIC data for the cortical stage and the SUNY data for the thalamic stage. CNRS-UNIC has provided the stimulation design to make both thalamic and cortical data directly comparable. This modelling study serves as a minimal architectural skeleton for a larger scale model to be developed later by CNRS-UNIC in HBP. This new model will include the intra-V1 and cortico-cortical connections and the identified cortical non-linearities, revealed by the experimental studies at UNIC.

3.5.2 Neural correlates of unimodal and multi-modal perception in mammalian primary sensory areas (T3.5.2)

3.5.2.1 Neuro-cognitive constraint of interest

Perception occurs through different senses that can interact with each other to ease the interpretation of the environment. In line with this psychological observation, both fMRI and electrophysiology have shown that many sensory areas of the brain, and in particular of the cortex, can be modulated by other sensory modalities than the modality to which they are mainly dedicated[61,62,63,64,65,66,67,68,69,70]. This represents a major constraint for the cognitive architectures underlying perception, indicating that sensory systems cannot be modelled as independent feed-forward processing channels.

3.5.2.2 General work plan

The ultimate goal of this task is to use the power of the model for functional circuit dissection to refine our knowledge of the computational role and the connections involved in multisensory interactions. This will facilitate the building of models that accurately account for low-level crosstalk between multisensory channels. The project proceeds in two steps corresponding to the two phases of HBP:

- 1st phase (Ramp-up 0-30 months): setting-up two high-density recording protocols during (a) passive and (b) active multisensory perception in the mouse and identifying computations performed by multisensory interactions in population representations of sensory stimuli.
- 2nd phase: Addressing optogenetically the connections that causally underlie multisensory interactions identified through these protocols.

3.5.2.3 Milestone at 6 months

Strategic question: Following movement of surrounding objects or beings is a crucial task for the brain. According to the literature, low level multisensory interactions particularly prominent for stimuli, which congruently signal motion of objects. We will design protocols to measure sensory cortex activity evoked by auditory and visual stimuli that mimic an object approaching or moving away from the subject, in order to test the impact of congruent or incongruent multisensory stimulation on the representation of the stimulus.

Protocols:

- The first protocol consists of measuring sensory representations in the auditory and visual cortex in passively attending awake mice, during presentation of 2-second sounds increasing or decreasing in amplitude or frequency combined with animated visual stimuli. The visual stimuli include disk increasing or decreasing in diameter (object moving towards or away) to test for global effects during motion of an object relative to the subject, and vertically moving gratings (up or down) to test for multisensory effects on direction sensitivity. Using superposition, we will also create ambiguous unimodal stimuli. In humans, specific activations of the brain occur during congruent sound increase and approach of a visual object[71]; moreover, direction perception can be biased by frequency modulated sounds[72]. We will therefore measure auditory and visual representations in the mouse based on population vectors of 1000 to 2000 recorded neurons across visual areas during unimodal and multimodal stimulation.
- This data set will allow us to answer the following questions: Do multimodal stimuli induce modifications of unimodal representations change of the population? Do these modifications reflect the congruency of the two modalities (e.g. boosting of response for approaching object and increasing sound amplitude)? Can one modality help disambiguate the representation of another modality (bias of the representation of an object marginally approaching when presented with a sound that signals an approach)?
- The second protocol is similar to the first one but includes active discrimination of the stimuli during imaging. This protocol consists in training mice to discriminate (a) gratings moving up or down paired with frequency modulated sounds (up vs. down modulation), (b) coming towards vs. moving away the animal congruently with a harmonic sound increasing in amplitude. Imaging during behaviour will allow us to test if the perception (shown through the animal response) correlates with cortical representations.

Current status: We have set up two-photon calcium imaging in the mouse visual and auditory cortex using genetically encoded sensors and acquired first test data. We have implemented the software for passive and active perception (stimuli + behavioural task). We have designed 50% of the stimuli. We have started to run the behavioural task in head fixed mice but we are currently improving the stimuli for optimal multisensory integration during behaviour.

3.6 Capabilities Characteristics of the Human Brain (WP3.6)

3.6.1 Linguistic and non-linguistic nested structures (T3.6.2)

3.6.1.1 Research goal

The purpose of this task led by Christophe Pallier (CEA) is to shed some light on the problem of how the human brain encodes tree structures – a neural code whose mechanisms are currently unknown, and which indeed has been hypothesised as perhaps unique to humans as opposed to other non-human primates[73]. To clarify which areas are involved and how they operate, we plan 3 studies (only partially funded by HBP).

3.6.1.2 Strategic experimental protocols

Experiment 1 will focus specifically on language, and will examine how fMRI signals vary as a function of the complexity of sentence structure. It will test models arising from linguistic theory. Arguments from linguistics suggest that sentences are not mere linear sequences of words, but are organised into hierarchical syntactic structures. The brain network implicated in the construction of such structures has been made evident by manipulating the size of syntactic constituents[74]. A second claim of the mainstream syntactic theory is that the syntactic structures of some sentences can contain unpronounced items called empty categories ("PRO, pro, wh- and np-traces"). These empty elements should be taken into consideration when computing the syntactic complexity of a sentence. We have generated sets of short sentences varying in the number of overt words and empty categories that they contain (from 0 to 3). These sentences will be presented visually to participants and 3T-fMRI will be used to measure activation as a function of numbers of covert and overt items (two pilot subjects have been run and the analyses are underway).

Experiments 2 and 3 will examine, behaviourally and with fMRI and MEG, how humans extract the regularities of sentences. It will test models arising from Bayesian learning theory and from Kolmogorov complexity theory. When exposed to any type of sequences, even random ones, humans search for regularities, like streaks and alternations. When these expectations are violated, surprise signals are detected in the brain (e.g. P300) and in behaviour. After reviewing the literature, we identified the need for an information-theoretic account of these surprise signals. We designed an ideal observer model for novelty detection, validated on existing seminal data from the literature. In Experiment 2, we plan to acquire new data with an extended version of the initial sequence protocol[75] to test predictions of our model and quantitatively compare it to existing models.

In Experiment 3, we plan to specifically test whether and how humans encode nested as opposed to serial regularities in sequences. To create non-trivial nested regularities outside the language domain, we designed a completely novel paradigm where a sequence of locations is presented visually, and sequence complexity is modulated by the number of (possibly nested) rules needed to encode (or compress) the sequence structure. For optimal comparability, all sequences use 8 locations on an octagon, but some sequences appear random (maximal complexity), some are compressible according to a nested rule of variable complexity, and some are only encodable as serial structures of variable length. We are comparing behaviour (anticipatory eye movements) and brain activity to those three types of sequences (random, nested or serial).

We have acquired adult eye-movement data, are starting data collection with adult human fMRI, and also plan (with non-HBP funding) to compare those data with similar data acquired in non-human primates. The outcome will reveal (a) whether non-linguistic sequences are encoded as serial or as nested structures, (b) which areas are involved, and (c) whether human and non-human primates differ in this respect.

3.6.1.3 Timeline for work process

- M6: For Experiment 1, the stimuli have been generated and the experimental stimulation programs have been written. Pilot fMRI data in three human participants have been acquired and are being analysed. Concerning Experiment 2, a thorough review of the literature has been completed and a model has been devised. For Study 3, we have acquired human adult eye-movement data.
- M12: Experiment 1: End of analysis of Pilot Data. We will reach 50% of acquisitions of main fMRI data.
- Experiment 2: Programming of the experiment and acquisition of pilot data.
- Experiment 3: We will have completed the eye-movement experiment and acquired 50% of the main fMRI data set in humans. The training of monkeys will start.
- M18: End of human fMRI acquisitions for all studies. Start of monkey fMRI acquisition for Study 3.
- M24: Completion of all data in human analyses.
- M30: Papers written and submitted.

3.6.2 The social brain – representing the self in relation to others (T3.6.3)

3.6.2.1 Research goal

This task will provide constraints for the emergence and shaping of the conscious mind, specifically to argue for the importance of other people in this process. The key scientific problem to tackle is whether smooth social interaction is the default mode of human brain function that enables social cognition (as we assume) or whether it is the result of bottom-up computations based on complex cognitive skills. The strategic experimental protocols will compare brain function during reactive, proactive and interactive states using simultaneous measurements of the brains of two interactors.

The group led by Riitta Hari (AALTO) will design and conduct neuroimaging experiments on humans to address these constraints. The experimental work will include fMRI and MEG measurements of single subjects using simplified social stimuli (movies of encounters, persons, faces, eyes) with the goal to study brain function in as naturalistic conditions as possible. In addition, simultaneous measurements of two interacting subjects will be conducted. These dual measurements allow us to highlight brain processes supporting social interaction by seeking for commonalities (e.g. synchrony) in the signals of the two brains, without reference to the typically complex behavioural patterns of the dyad.

3.6.2.2 Timeline for work process

This task will start at Month 9. The following plan is envisaged:

- M12: Definition of the architectural question completed. Design for a new social localiser for fMRI (and MEG) completed, and a draft localiser constructed. An invited review paper on the brain basis of social interaction completed for Clinical Neurophysiology.
- M18: The localiser has been finalised, piloted, and run on 12–15 subjects. Data analysis has been started. Discussions about the cognitive architecture of social interaction have been completed with Task 3.1.2 leader (Martin Giese).

- M24: The data analysis of the fMRI social localiser experiment is completed. The two-MEG-setting has been used to test the interactive brain hypothesis (in contrast to assuming that two interacting brains act in mutually-reactive mode only).
- M30: Data analysis completed for the two-MEG study. List of neurocognitive constrains of cognitive architectures underlying social interaction has been constructed.

4. Measuring Progress

The progress of work is measured using Key Performance Indicators as determined in the HBP Description of Work. Coordination Work Package 3.7 will evaluate the progression of experimental data acquisition by examining how far research has progressed on the following scale:

- Definition of a strategic theory-relevant experiment, given the existing literature
- Experimental design
- Generation of stimuli
- Programming of the experiment
- Pilot data
- Acquisition of full data set
- Programming of data analyses
- Generation of definitive results
- Paper publication

The progression of simulation models (relevant only for a subset of the proposed cognitive architectures) will be evaluated according to the following scale (see T3.1.2 led by Martin Giese and WP3.4 led by Neil Burgess):

- Definition of strategic data for modelling, given the existing literature
- Simulation design
- Pilot simulation data
- Generation of definitive results
- Comparison with strategic data
- Paper publication

Finally, progress in defining synthetic summaries of neuro-cognitive constraints on cognitive architectures will be evaluated according to the number of syntheses and, for each of them, the following criteria:

- Isolation of relevant data
- Write-up
- Synthesis and, if appropriate, corresponding data put in appropriate form on the HBP KnowledgeSpace
- Validation by one or more external referees

Expected times of delivery from each team are defined in the following table for each Task in SP3.

Table 1: Categorical Stage Indicators for SP3

WP3.1	Perception - Action	M6	M12	M18	M24	M30
T3.1.1	**Study of the circuits involved in non-conscious and conscious mechanisms of visual recognition**					
	Definition of a strategic question, given the existing literature	50%	100%			
	Experimental design		100%			
	Generation of stimuli		50%	100%		
	Programming of the experiment		50%	100%		
	Pilot data		50%	100%		
	Acquisition of full data set				50%	100%
	Programming of data analyses				50%	100%
	Generation of definitive results					100%
T3.1.2	**Understanding the circuits linking perceptions to actions**					
	Definition of a strategic question, given the existing literature	100%				
	Simulation design		100%			
	Programming of data analyses	20%	40%	60%	80%	100%
	Generation of definitive results	0%	10%	30%	50%	100%
	Write-up of paper				50%	100%

WP3.1 (cont'd)	Perception - Action	M6	M12	M18	M24	M30
T3.1.3	**Understanding how body perception becomes a reference point for the sense of self**					
	Definition of a strategic question, given the existing literature	50%	100%			
	Experimental design	100%				
	Generation of stimuli	100%				
	Programming of the experiment	100%				
	Pilot data	100%				
	Acquisition of full data set		50%	100%		
	Programming of data analyses		50%	100%		
	Generation of definitive results				50%	100%
	Write-up of paper	5%	10%	15%	50%	100%
WP3.2	Motivation, Decision and Reward	M6	M12	M18	M24	M30
T3.2.1	**Mapping and understanding the neuronal circuits involved in decision making, confidence and error correction**					
	Definition of a strategic question, given the existing literature	60%	90%	100%		
	Experimental design	40%	70%	100%		
	Generation of stimuli	30%	60%	100%		

WP3.2 (cont'd)	Motivation, Decision and Reward	M6	M12	M18	M24	M30
T3.2.1 (cont'd)	**Mapping and understanding the neuronal circuits involved in decision making, confidence and error correction**					
	Programming of the experiment	30%	60%	100%		
	Pilot data	20%	50%	80%	100%	
	Acquisition of full data set	0%	10%	40%	80%	100%
	Programming of data analyses	20%	40%	60%	80%	100%
	Generation of definitive results	10%	30%	50%	70%	100%
	Write-up of paper	20%	50%	60%	80%	100%
T3.2.2	**Mapping and understanding the neuronal circuits involved in motivation, emotion and reward**					
	Definition of a strategic question, given the existing literature			100%		
	Experimental design			100%		
	Generation of stimuli			100%		
	Programming of the experiment			100%		
	Pilot data			100%		
	Acquisition of full data set			50%	75%	100%
	Programming of data analyses					100%
	Generation of definitive results				50%	100%

WP3.2 (cont'd)	Motivation, Decision and Reward	M6	M12	M18	M24	M30
T3.2.2 (cont'd)	**Mapping and understanding the neuronal circuits involved in motivation, emotion and reward**					
	Write-up of paper				50%	100%
WP3.3	**Learning and Memory**	M6	M12	M18	M24	M30
T3.3.1	**Skills and habits**					
Experi-ment 1	Brain signatures of motor skill consolidation in young healthy human adults (fMRI study)					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	100%				
	Generation of stimuli	100%				
	Programming of the experiment	100%				
	Pilot data		100%			
	Acquisition of full data set			100%		
	Programming of data analyses		100%			
	Generation of definitive results				100%	
	Write-up of paper				100%	

WP3.3 (cont'd)	Learning and Memory	M6	M12	M18	M24	M30
T3.3.1 (cont'd)	**Skills and habits**					
Experi-ment 2	Differential effects of observation and actual movement performance on procedural memory consolidation (fMRI study, Behaviour)					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	100%				
	Generation of stimuli	100%				
	Programming of the experiment	100%				
	Pilot data		100%			
	Acquisition of full data set			100%		
	Programming of data analyses			100%		
	Generation of definitive results				100%	
	Write-up of paper					100%
T3.3.2	**Memory for facts and events**					
	Definition of a strategic question, given the existing literature	35%	70%	100%		
	Experimental design	25%	50%	75%	100%	
	Generation of stimuli	25%	50%	80%	100%	
	Programming of the experiment	25%	35%	80%	100%	
	Pilot data	25%	35%	80%	100%	

WP3.3 (cont'd)	Learning and Memory	M6	M12	M18	M24	M30
T3.3.2 (cont'd)	**Memory for facts and events**					
	Acquisition of full data set	5%	20%	35%	70%	100%
	Programming of data analyses	5%	20%	30%	90%	100%
	Generation of definitive results	5%	10%	20%	50%	100%
	Write-up of paper (several papers written along the line, not only one paper)	5%	10%	20%	50%	100%
T3.3.3	**Working memory**					
	Definition of a strategic question, given the existing literature	90%	100%			
	Experimental design	50%	100%			
	Generation of stimuli		100%			
	Programming of the experiment		100%			
	Pilot data		50%	100%		
	Acquisition of full data set			100%		
	Programming of data analyses			100%		
	Generation of definitive results			100%		
	Write-up of paper			50%	100%	

WP3.4	Space, time and numbers	M6	M12	M18	M24	M30
T3.4.1	**Model of hippocampal navigation**					
	Review of sensory and self-motion information in self-localisation and place and grid cell firing	100%				
	Definition of strategic data for modelling based on existing literature	50%	100%			
	Design of simulations	30%	60%	80%	90%	100%
	Pilot simulation data	25%	50%	75%	100%	
	Inclusion of firing of place, head direction and grid cells	25%	50%	75%	100%	
	Generation of definitive results		25%	50%	75%	100%
	Paper publication			25%	50%	75%
T3.4.2	**Model of striatal navigation**					
	Definition of strategic data for modelling, given the existing literature		50%	100%		
	Simulation design		50%	100%		
	Pilot simulation data		20%	50%	100%	
	Generation of definitive results		25%	50%	75%	100%
	Integration with hippocampal navigation model		25%	50%	75%	100%
	Paper publication			25%	50%	75%

WP3.5	From sensory processing to multimodal perception	M6	M12	M18	M24	M30
T3.5.1	**Neural correlates of unimodal perception and self-organisation of internal knowledge in mammalian primary cortical areas**					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	50%	100%			
	Generation of stimuli	50%	50%	75%	100%	
	Programming of the experiment	50%	75%	75%	100%	
	Pilot data	50%	75%	100%		
	Acquisition of full data set		25%	50%	100%	
	Programming of data analyses	50%	50%	50%	100%	
	Generation of definitive results			50%	100%	
	Write-up of paper	100% (P1) 50% (P2)			50% (P3)	100% (P1-3)
T3.5.2	**Neural correlates of unimodal and multi-modal perception in mammalian primary sensory areas**					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	50%	100%			
	Generation of stimuli	50%	100%			
	Programming of the experiment	50%	100%			

WP3.5 (cont'd)	From sensory processing to multimodal perception	M6	M12	M18	M24	M30
T3.5.2 (cont'd)	**Neural correlates of unimodal and multi-modal perception in mammalian primary sensory areas**					
	Pilot data		50%	100%		
	Acquisition of full data set		25%	75%	100%	
	Programming of data analyses			50%	100%	
	Generation of definitive results				90%	100%
	Write-up of paper				50%	100%
WP 3.6	Capabilities characteristic of the human brain	M6	M12	M18	M24	M30
T3.6.1	**Symbols and their manipulation**					
T3.6.2	**Linguistic and non-linguistic nested structures**					
Experi-ment 1	Syntactic Complexity of sentences: the role of empty categories					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	100%				
	Generation of stimuli	100%				
	Programming of the experiment	100%				
	Pilot data	50%	100%			
	Acquisition of full data set	0%	50%	100%		
	Programming of data analyses	10%	50%	80%	100%	

WP3.6 (cont'd)	Capabilities characteristic of the human brain	M6	M12	M18	M24	M30
T3.6.2 (cont'd)	**Linguistic and non-linguistic nested structures**					
	Generation of definitive results	0%	0%	80%	100%	
	Write-up of paper	0%	0%	50%	80%	100%
Experi-ment 2	Bayesian Modelling of Expectation Effects in Sequences					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	50%				
	Generation of stimuli	50%	100%			
	Programming of the experiment	0%	100%			
	Pilot data	0%	100%			
	Acquisition of full data set	0%	0%	50%	100%	
	Programming of data analyses	0%	0%	50%	100%	
	Generation of definitive results	0%	0%	0%	100%	
	Write-up of paper	0%	0%	50%	80%	100%
Experi-ment 3	Bayesian Modelling of Expectation Effects in Sequences					
	Definition of a strategic question, given the existing literature	100%				
	Experimental design	100%				
	Generation of stimuli	100%				
	Programming of the experiment	100%				

WP3.6 (cont'd)	Capabilities characteristic of the human brain	M6	M12	M18	M24	M30
T3.6.2 (cont'd)	**Linguistic and non-linguistic nested structures**					
	Pilot data	10%	100%			
	Acquisition of full data set	0%	50%	100%		
	Programming of data analyses	10%	50%	80%	100%	
	Generation of definitive results	0%	0%	80%	100%	
	Write-up of paper	0%	0%	50%	80	100
T 3.6.3	**The social brain – representing the self in relation to others**					
	Definition of a strategic question, given the existing literature		60%	100%		
	Experimental design		60%	100%		
	Generation of stimuli		60%	100%		
	Programming of the experiment		60%	100%		
	Pilot data		5%	80%	100%	
	Acquisition of full data set			20%	80%	100%
	Programming of data analyses				20%	100%
	Generation of definitive results		5%	10%	40%	100%
	Write-up of paper				25%	75%

5. Conclusions

This document demonstrates that in the ramp-up phase, SP3 is developing the methods for functional mapping along clear indicators of progress and target values. The document defines the purpose of each SP3 task, as well as the organisation of the work and the interactions with other SPs in the HBP. The Key Performance Indicators are clearly defined according to the HBP requirements.

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