Early version of use case for cognitive performance integrating data and models (D2.2 - SGA3)

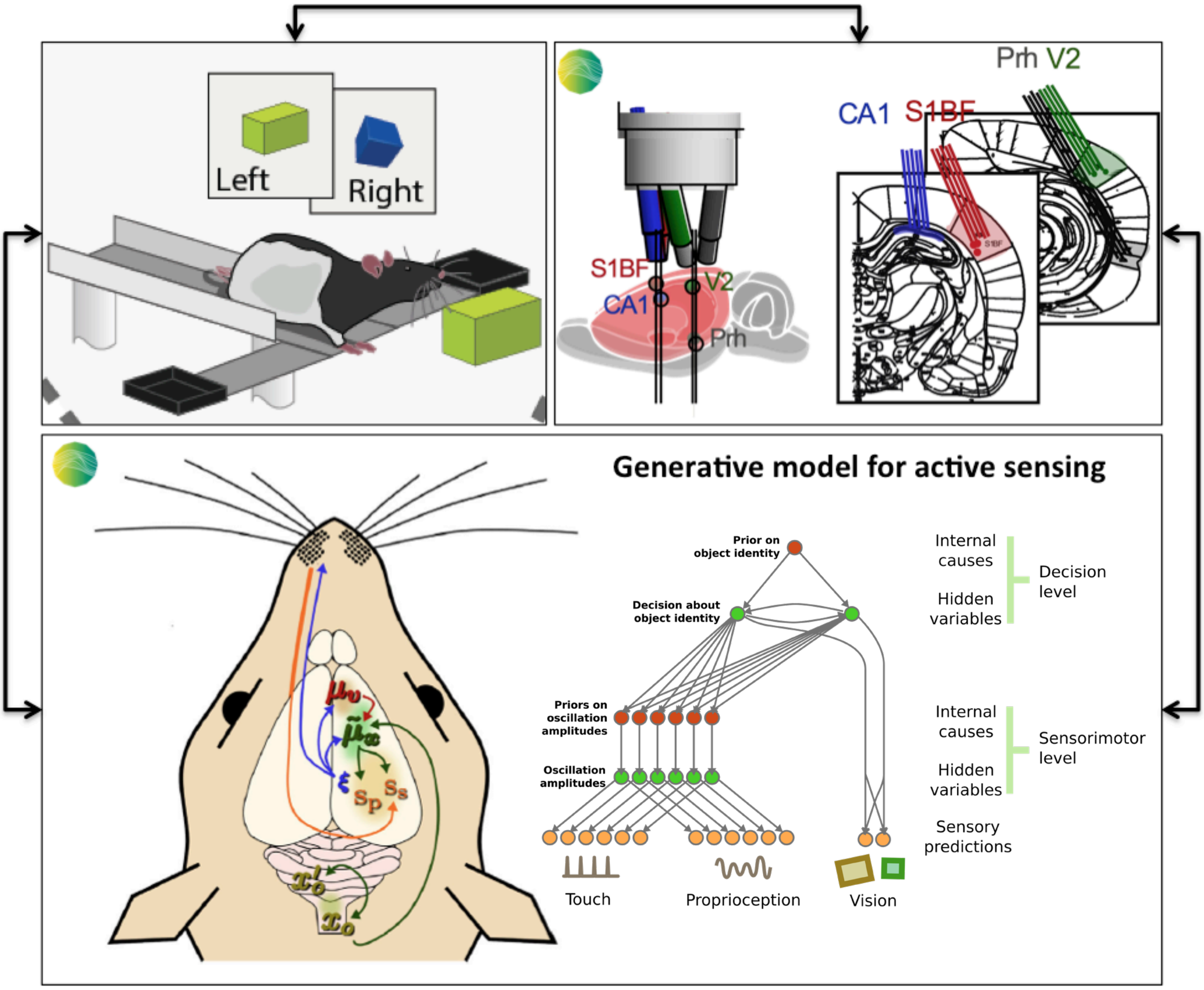

Figure 1: An integrative perspective on multisensory object recognition.

The top-left panel illustrates schematically the behavioural task that we use to study multisensory object recognition in rodents. The top-right panel illustrates the ensemble recording approach to record simultaneously from four brain areas: barrel cortex (S1BF), secondary visual cortex (V2), perirhinal cortex (Prh) and the hippocampal area CA1. The bottom panel provides a sketch of the computational modelling approach to study anticipatory dynamics in whisker movements and the putative neuronal correlates of proprioceptive, somatosensory, and visual predictions and prediction errors in the brain. The right part of the panel shows the generative model used to implement active sensing in an active inference agent, whereas the left panel shows the putative neuronal underpinnings of the model variables in the rodent brain. The symbols that appear in the schematic denote proprioceptive and somatosensory predictions (Sp and Ss), hidden state variables (x) and causal variables (v) of the model, whereas the symbols μ and ξ denote mean values of model variables and prediction errors, respectively. See (Mannella et al., 2021) for details on a preliminary version of the model. The EBRAINS logos indicate that the EBRAINS infrastructure affords the storage and processing of both neural data and models.

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Description in GA:	This early Deliverable will present an early version of an integrated use case for object recognition including existing data and models as well as specific planning for development ranging from experimental data to models, neuromorphic implementations, and potential uses in robotics.
Abstract:	In this work research groups from the UvA and CNR collaboratively investigate the neural mechanisms underlying tactile sensation. A model has been developed by the CNR research group explaining whisking dynamics using active inference. The model will be used to analyse and explain neural activity recorded in rodents during a sensory discrimination task. The product of this work will be Live Paper 2.1a, which is titled "Active inference in tactile sensing during multisensory object recognition".
Keywords:	Tactile sensation, active inference, rodent whisking, modelling, predictive coding, ensemble recordings.
Target Users/Readers:	Computational neuroscience community, computer scientists, consortium members, experts in somatosensation, neuroscientific community, neuroscientists, researchers, scientific community.

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History of Changes made to this Deliverable (post Submission)

Date	Change Requested / Change Made / Other Action
26.11.2021	Draft Deliverable submitted to EC
22.06.2022	Deliverable submitted to EC
06.12.2023	Revised deliverable sent by WP to PCO. Main changes made, with indication where each change was made: • Update file name (correct deliverable number according to EC portal (D13) • Addition of behavioural protocol link (see Section 2) • Update of Looking Forward section (see Section 4)
06.12.2023	Revised version resubmitted to EC by PCO via SyGMa

1. Introduction

The work described in this Deliverable covers our current efforts within the HBP to provide an integrative perspective on multisensory object recognition that combines empirical evidence and computational modelling of active whisking. This objective addresses directly the central goal of HBP (and WP2 in particular) to advance our understanding of the functioning and neuronal underpinnings of advanced cognitive functions, such as multisensory perception.

The specific case study presented in this Deliverable is a multisensory object recognition task developed by the University of Amsterdam (UvA), in which rodents were presented each trial with one of two objects ("cube" or " parallelepiped") which they had to correctly recognise, by using only vision (visual trials), only whisking (tactile trials) or both vision and whisking (visuo-tactile trials).

This document will cover both the experimental results of the multisensory object recognition task and a computational model of the same scenario, which was realised by the National Research Council (CNR). Both the experiment and the computational model have been developed to test whether in rodents, visual and whisker-based exploration of the objects is guided by a process of prediction error minimisation and whether it is possible to identify neural signatures of prior and current predictive representations and prediction errors in sensory and higher-order regions of the rodent brain.

Notably, the work described in this Deliverable will culminate in the Live Paper 2.1a on "Active inference in tactile sensing during multisensory object recognition". The "Live Paper" format will permit the readers to actively explore and interact with both the (neurophysiological and kinematic) data from the rodent experiment and the computational model. For this, the paper will include "Live Figures" that will allow the readers to explore different ways in which data can be grouped and plotted and to change several parameters of the computational model, to study which parameterisations explain kinematic and neural data better.

This work links to the EBRAINS research infrastructure in the following ways: 1) it uses the Data and Knowledge Graph service that stores neurophysiological data, and uses EBRAINS brain atlases, see e.g. (Bjerke et al., 2018); 2) it uses computing facilities of EBRAINS to run the computational models and analyse the empirical neural data; Hence this paper uses the EBRAINS infrastructure by using our dataset stored in the Knowledge Graph. The dataset itself is processed and curated using dedicated HBP tools. The electrophysiological data is formatted in the universal Neo format (a Python toolbox for the management of ephys data); the analysis of the neural data is performed with the Python Elephant toolbox in EBRAINS, and the anatomical data is aligned to the rodent reference atlas in EBRAINS. The Live Paper 2.1a will primarily contribute to the Modelling areas (Service Categories) of the HBP. Please note that all the data, models, and software to extract features from data described in this deliverable will be made fully available in EBRAINS during the process of submission of the Live Paper 2.1a.

The communities that will be most interested in the Live Paper are neurophysiologists and computational modellers interested in systems neuroscience.

2. Multisensory object recognition task

This section describes the multisensory object recognition task developed by UvA. Below we briefly summarise the task and data analyses.

2.1 Experiment set-up and scientific rationale

In the multisensory object recognition task, rats were presented each trial with one of two possible objects (henceforth, "cube" or "parallelepiped") when they were at the decision point of a T-maze. Then, they had to choose one of two sides of the maze and received sucrose reward after correctly poking the side associated with the correct object, see Figure 2.

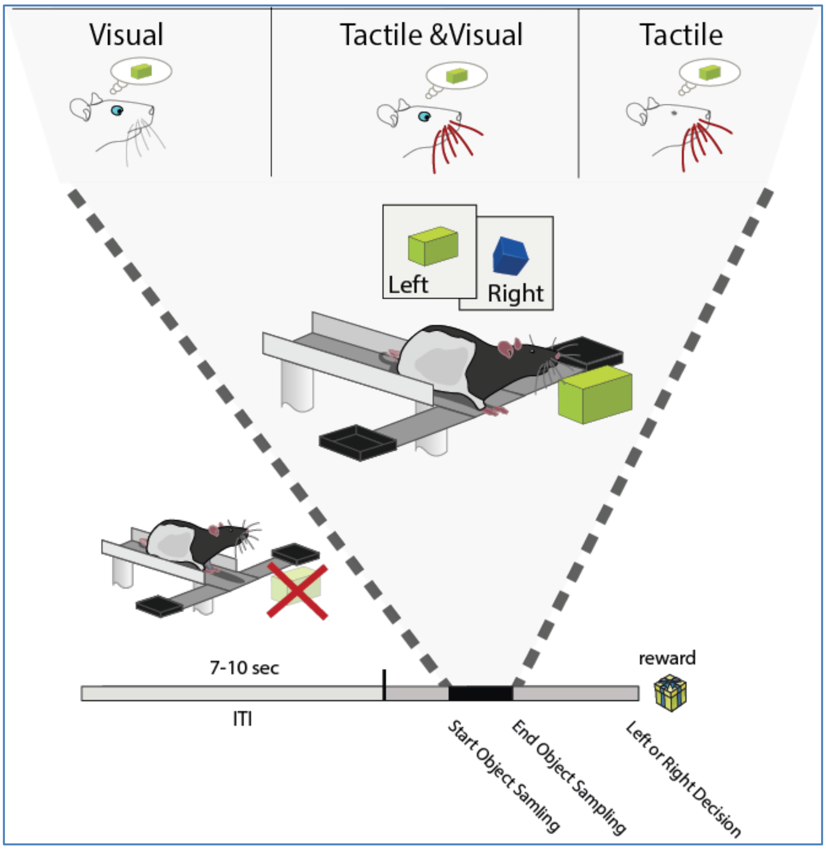

Figure 2: The multisensory object recognition task.

A behavioural trial consists of an inter-trial interval (ITI), a sampling and a decision epoch. During the sampling epoch the object was presented either in the Visual, Tactile or Multimodal (Tactile and Visual) modality. The rat was tasked to make a poke on the arm associated with either object.

Crucially, the task included three (randomly presented) kinds of trials: Visual trials, in which the light was on, but the object was further away and not reachable by whiskers; Tactile trials, in which the light was off, but the object was within reach of whiskers; and Visuo-Tactile trials, in which the light was on, and the object was close by. The presence of these three kinds of trials permits studying the differences between unimodal (Visual or Tactile) and multimodal (Visuo-Tactile) situations. The behavioural protocol for the task has been described in the Knowledge graph: https://search.kg.ebrains.eu/?category=Contributor&q=julien#452d5de0-99c2-4505-b00a-9e305b6e27ed.

During the experiments, whisking kinematics were recorded using a high-speed camera, which permits tracing whisker movements and the time of contact with the objects. In parallel, simultaneous single unit recordings and local field potential were collected from two sensory cortical areas (barrel cortex, sbf1, and visual cortex, V2; cf. Oude Lohuis et al. 2022) and two medial temporal lobe structures (hippocampal area CA1 and perirhinal cortex) that we hypothesise to be crucial in the formation and retrieval of multimodal memories (Bos et al., 2017; Vinck et al., 2016).

The scientific hypotheses that we are most interested in testing is 1) whether visual and whisker-based exploration of the objects is guided by a process of prediction error minimisation, as postulated by theories of predictive coding and active inference; and 2) whether neural signatures of prior predictions and prediction errors on object locations and dimensions are computed locally in sensory structures, such as the barrel cortex and/or higher-order regions, such as the medial temporal lobe, and the hippocampus.

2.2 Data analyses

Together with EBRAINS, we make a joint effort between UvA and CNR to analyse the experimental data stemming from the multisensory object recognition task. Below we summarise our current advancements in the analysis of kinematic and neurophysiological data.

2.2.1 Analysis of kinematic data

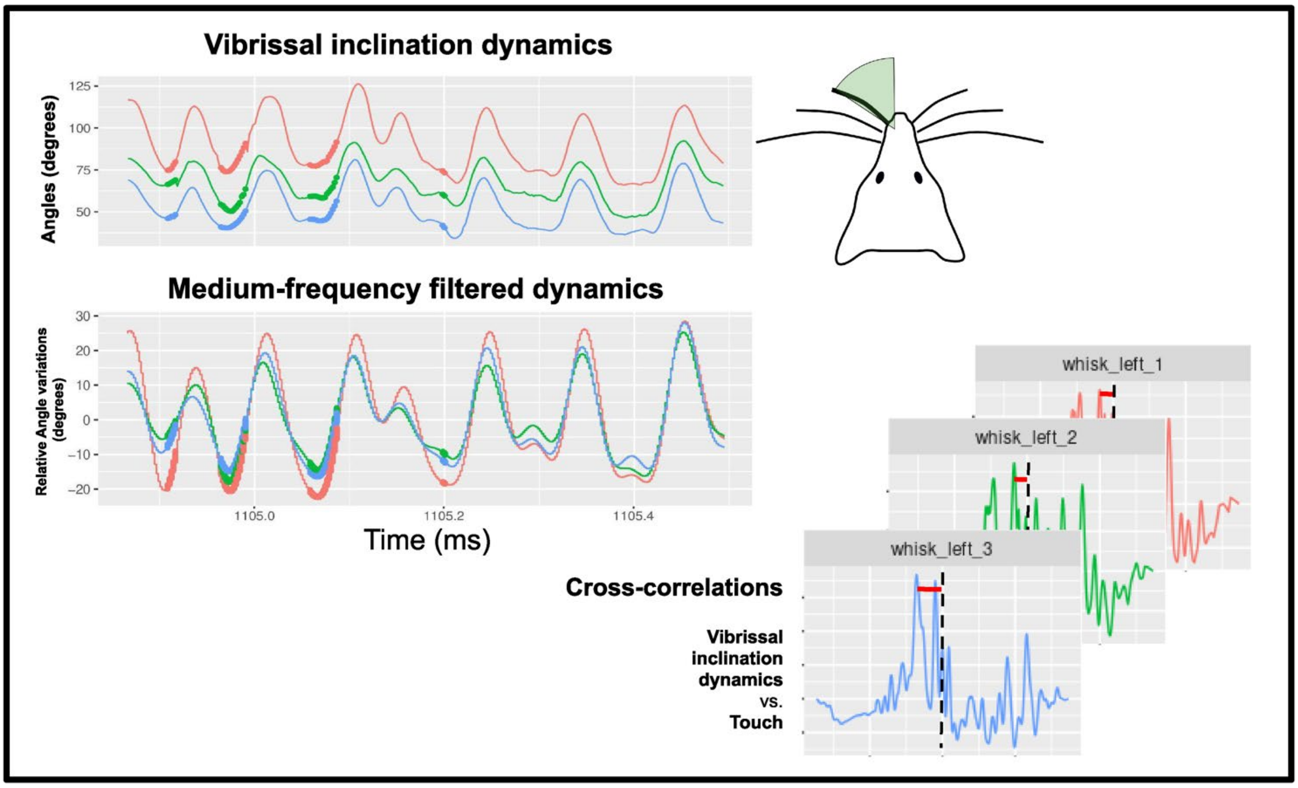

Figure 3: Schematic of the analysis of kinematic data.

This figure illustrates the approach to the analysis of whisking kinematics. The left panels illustrate sample whisker dynamics (with or without filtering). The Y-axis denotes angles (top) or angle differences (bottom) whereas the X-axis denotes time. The bottom-right panels illustrate examples of cross-correlations between whisker dynamics and touch events, which permit measuring anticipatory and reactive aspects of whisking. See the main text for explanation.

The aim of the analysis of whisking kinematics is twofold. First, finding a measure able to discriminate situations in which whisking behaviour is adjusted in an anticipatory manner (to reflect an expectation of object touch) versus adjusted in a reactive manner, as a reaction to an unexpected touch. Second, assessing the ratio of the amount of anticipatory versus reactive whisking behaviours in different trials (Tactile vs Visuo-Tactile trials).

The original data, extracted from video recordings by UvA, consist of the time series of the dynamics of 6 whiskers (see Figure 3). Whiskers are chosen so that 3 whiskers are part of the left whisker pad, and the other 3 whiskers are in the respective position in the right whisker pad. Dynamics represent the angular inclination at each time interval of a trial of each whisker with respect to the head. These time-series are extracted for each trial within the Visual, Visuo-Tactile and Tactile conditions. The data also include the two time-series of touch events for each trial, accounting for touches by the left and right groups of whiskers, respectively.

To analyse the data, CNR developed a novel measure of anticipation/reaction, using standard Python libraries for statistical analysis (SciPy and Pandas). The anticipation/reaction measure considers the cross-correlations between whisking time-series (filtered at their most informative range of frequencies) and touching time-series. Lags from 0 to the maximum number of spikes in the cross correlograms are considered. These scores convey information about the temporal correlations, indicating which of the timeseries must be shifted forward in time to obtain higher correlation. Thus, they can be used to build a measure of the temporal anticipation of touch events through whisker dynamics. We are currently refining this measure to test the hypothesis that the animals adjust their whiskers in an anticipatory manner and anticipatory dynamics are especially prominent during Visual Trials, in which the animals can use visual information to correct their sensorimotor model before acquiring any somatosensory information.

As explained below, a further step will be to put these data in relation with those simulated by an active inference model of rat behaviour, whose hierarchical generative model is made up by a sensorimotor layer and a decision-making layer, which generates predictions about the kind of object that is currently observed.

2.2.2 Analysis of neural data

To investigate the neural mechanisms driving sensory detection, the effect of behavioural parameters (such as sensory modality) on neural activity is studied. An example of this analysis is the encoding model depicted in Figure 4. Such a model fits the behavioural parameters on the neural data, highlighting the contribution of individual behavioural parameters. If for instance modality were to be an import driver for neural activity in the investigated area, then the behavioural parameters for stimulus presentation and modality will contribute more to the generation or explanation of neural activity. This analysis allows us to include other parameters such as the prediction signal generated by the computational model described in Section 3. All our analyses are written in Python, the source code will be published together with the Live Paper 2.1a and users can run the pipeline on EBRAINS using their own parameters. The analysis will depend on HBP data-processing packages such as Neo and Elephant and other open-source libraries for python.

Further, the data will be analysed with respect to spike and local field potential (LFP) interactions. Previously it has been shown that neurons lock their firing on the whisking kinematics of rats (Grion et al., 2016). The contribution of a prediction signal as described by the model in Section 3 to this interaction will be investigated.

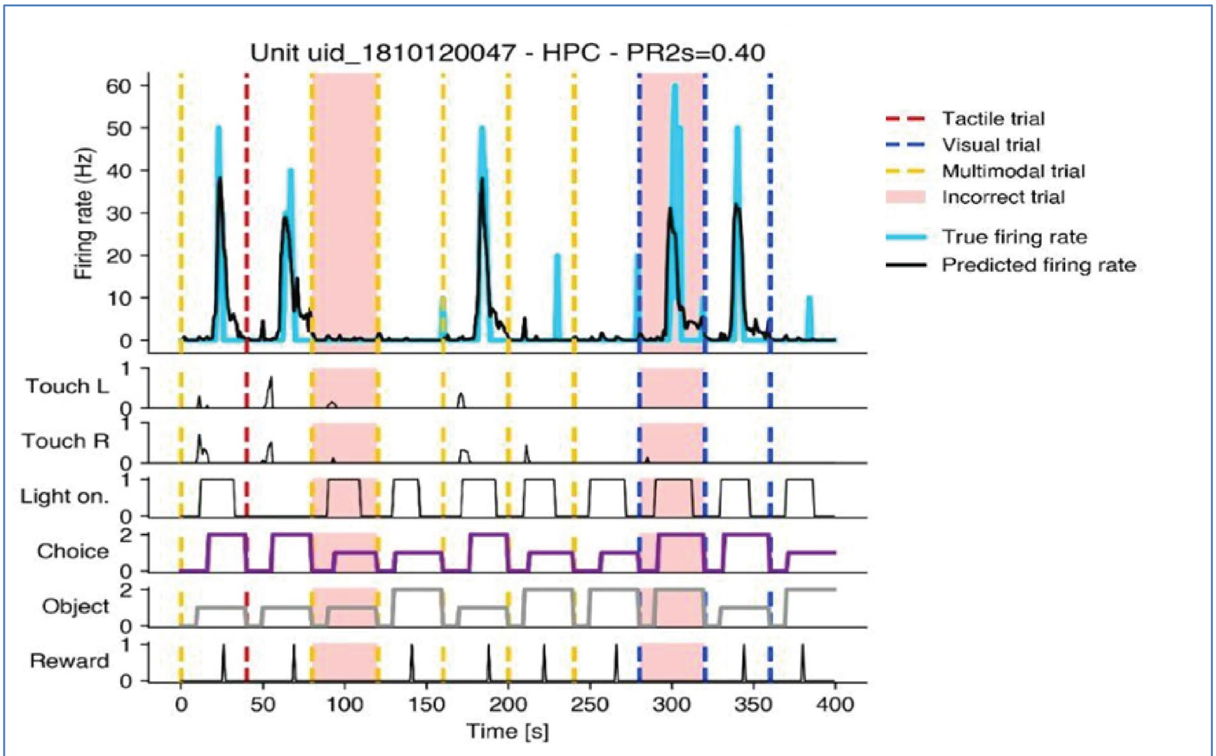

Figure 4: Figure illustrating the analysis of neural data.

The firing rate of a single unit is nearly replicated by the prediction signal of the encoder model (blue and black traces in the top row, respectively). The encoder model uses behavioural parameters (black, bottom rows) to predict neural activity.

3. Computational model of active whisking

The Live Paper will include the description of a computational model of active whisking based on the framework of active inference, which describes action and perception as guided by an overall process of minimisation of prediction errors (Friston, 2005; Rao & Ballard, 1999); or more formally, a minimisation of variational free energy (Friston, 2010; Parr et al., 2022). The computational model used for the Live Paper will be an extension of the recently published model of (Mannella et al., 2021) and is realised in Python.

3.1 Brief illustration of the computational model

The computational model is inspired by previous findings about how rats and mice adapt their whisking kinematics to optimise their whisker placement during tactile sensing. Across several studies, it emerged that rats and mice use an anticipatory strategy to adapt their whisker amplitude to the distance (and location) in which they expect to encounter objects (Voigts et al., 2015). In other words, they might form an internal prediction based on a (memorised) expectation of the location of an object and adapt their whisking behaviour accordingly. To explain these findings, we adopt an active inference perspective and hypothesize that the brain generates object-specific predictions about whisker protractions and touches and treats unexpected whisker contacts as prediction error signals (discrepancies between the expectation and reality), to be minimised by adjusting whisker behaviour.

Figure 5 provides a schematic illustration of the computational model (left panel) and of some of the "synthetic time series" that the model can generate during whisking-based exploration (right panel); see (Mannella et al., 2021) for a detailed description of a preliminary version of the model. The left panel of Figure 5 shows the graphical model (Bayesian net) of the model. The nodes denote the (multimodal) model variables, which comprise sensory predictions in three modalities (proprioception, touch, and vision), hidden variables and internal motor causes (that modulate whisker amplitude). A key assumption of the model is that the animal uses an active sensing strategy to recognise objects. It initially sets whisker amplitude according to prior predictions about object identity and location (derived for example from visual information, if available); and continuously adjusts whisker movements to minimise prediction errors (e.g., unexpected touches). In turn, this prediction error minimisation process ensures that the animal has accurate predictions about object location and identity - hence effectively "recognising" it. Compared to the published study of (Mannella et al., 2021), the computational model used in the Live Paper includes two main novel elements that are key to model rodent multisensory object recognition data. The first novel element is a "visual stream" that processes visual information about the two objects present in the task. The second novel element is a decision-making system that is responsible for the final choice that the animal does in the task: moving to one of the two sides of the T-maze. The computational model used in the Live Paper 2.1a is therefore a hierarchical model that comprises a sensorimotor layer (guiding visual and whisker-based exploration) and a decision-making layer.

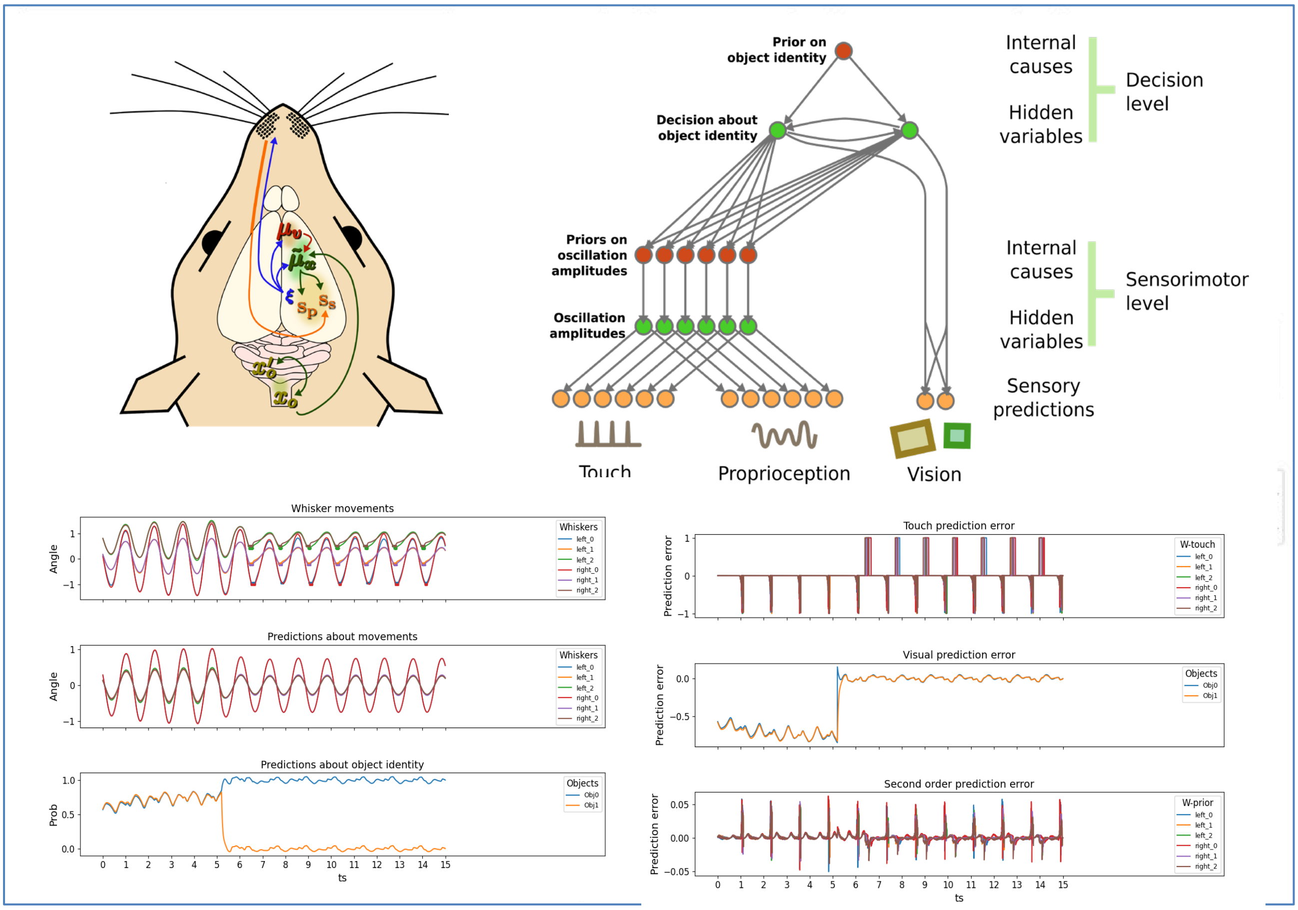

Figure 5: Computational model.

Top-right panel: schematic of the generative model used by the active inference agent. The computational model is hierarchical and includes a lower-level (sensorimotor) layer that includes three modalities: touch, proprioception, and vision. Furthermore, it includes a higher-level (decision) layer that is responsible to make decisions about object identity based on sensorimotor information gathered during visual and/or whisker-based exploration. Top-left panel: simplified neuronal implementation of the generative modelling scheme in the rodent brain. The symbols that appear in the schematic denote proprioceptive and somatosensory predictions (Sp and Ss), hidden state variables (x) and causal variables (v) of the model; whereas the symbols μ and ξ that appear in the bottom-left schematic denote mean values of model variables and prediction errors, respectively. See (Mannella et al., 2021) for details on the model. Bottom panel: "synthetic time series" generated from the model, by plotting how the model variables (e.g., predictions and prediction errors) vary over time during multisensory object recognition. The model-based analysis consists in using the "synthetic time series" generated by the model in the different conditions (e.g., Visual, Visuo-Tactile or Tactile) as predictors of rodents' neural activity in the same conditions. Figure contains head of the mouse from (top left) from Mannella et al.2021.

The right panel of Figure 5 shows some "synthetic time series" of the model variables (e.g., hidden states, somatosensory visual and second order prediction errors - errors between priors in the sensorimotor layer and generated priors in the decision layer) during an example episode of object exploration. These "synthetic time series" will become important in the model-based analyses of the experimental results of the multisensory object recognition task, as explained below.

3.2 Model-based data analysis

The main usage of the computational model is supporting "model-based data analysis". For this, we will use the "synthetic time series" that emerge from internal parameters of the computational model (e.g., predictions and prediction errors) as predictors of time series that emerged from the neural recordings in rodents - when the animal and the computational model are facing the same task. This analysis is done using custom-written Python software, which will be published on EBRAINS together with the Live Paper.

Specifically, we will firstly match the (whisking) behaviour of our model with the behaviour of animals that face the same kind of trials (e.g., the recognition of the Cube object during Tactile trials). To establish this matching, we will use the anticipation/reaction measure described above (in the analysis of kinematic data). Having established a matching between animal and model behaviour, and under the assumption that whisker kinematics reflect the expectancy of rats, our active inference model will be able to compute "synthetic time series": predictions and prediction errors based on whisking kinematics and other body parameters of the rat during each trial. This allows us testing to what extent the parameters (e.g., predictions and prediction errors) extracted from the model explain neural data in the four brain areas that were simultaneously recorded (barrel cortex, visual cortex, hippocampus and perirhinal cortex) - which would amount to asking to what extent these four areas show signatures of a prediction error minimisation process, as we hypothesise.

In sum, the model will be used to complement the data analysis approach illustrated in Figure 4, with additional predictors (that cannot be directly observed but only inferred with the aid of a computational model). The final model is available in the Knowledge Graph[1].

4. Looking Forward

In this document, we described a rodent multisensory object recognition task (Section 2) and a computational model (Section 3) developed to analyse the results, at both behavioural and neural levels. This empirical and computational work will form the core of the Live Paper 2.1a. In the Live Paper, we will test the idea that to recognise objects, rodents use an active whisking strategy that is guided by predictions and prediction errors (as described in Section 3) and - crucially - neuronal signatures of predictions and prediction errors can be found across the four brain areas that we recorded. To test this hypothesis, we validated the capability of the model to reproduce whisker behaviour, trial-by-trial; the model is able to generate synthetic time series for predictions and prediction errors that can be used to identify signatures of the same processes in the neuronal populations that we recorded, again trial-by-trial. The computational model is already able to reproduce whisker behaviour and generate synthetic time series (see Section 3). However, to achieve the ambitious goal of the Live Paper 2.1a, our current modelling work focuses on the fine-tuning of the part of the generative model that guides whisker movements, to ensure that the synthetic movements generated by the model align very accurately with the real whisker dynamics of rodents (a correct matching at the behavioural level is a key prerequisite for an accurate neural-level analysis).

All of the work described in this Deliverable (data analysis, computational modelling, "alignment" of model and data) is currently under development and is at different stages of completion. The computational model can be found here: https://search.kg.ebrains.eu/instances/3034a3bc-dd52-440c-a7e5-23104ebf36de. The data analyses, computational model, and alignment of model and data are finished. The most advanced results will be part of Live Paper 2.1a (the advanced draft has been discussed and reviewed internally, and as a result refinements and improvements are being conducted before submission to a peer-reviewed journal in the coming weeks). Deliverable D2.2 has been affected by consequences of data collection speed on model integration, and limited lab access due to COVID-19 restrictions both at the UvA (the Netherlands) as well as CNR (Italy).

[1] https://search.kg.ebrains.eu/instances/3034a3bc-dd52-440c-a7e5-23104ebf36de

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5.1 HBP Publications

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P2988: Parr, T., Pezzulo, G., & Friston, K. J. (2022). Active Inference: The Free Energy Principle in Mind, Brain, and Behavior. MIT Press.

P2862 Oude Lohuis M, Pie J, De Kock C, Pennartz CMA, Olcese U (2022) Task complexity temporally extends the causal requirement for visual cortex in perception. Pre-print BioXRev.

P3268 Matthijs N. Oude Lohuis, Jean L. Pie, Pietro Marchesi, Jorrit S. Montijn, Christiaan P. J. de Kock, Cyriel M. A. Pennartz & Umberto Olcese. Multisensory task demands temporally extend the causal requirement for visual cortex in perception. Nature Communications 13, 1:2864. https://doi.org/10.1038/s41467-022-30600-4

5.2 Other

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