Journal of Neuroscience Methods 242 (2015) 1–14

Contents lists available at ScienceDirect

Journal of Neuroscience Methods

journal homepage: www.elsevier.com/locate/jneumeth

Computational Neuroscience

Active inference and oculomotor pursuit: The dynamic causal modelling of eye movements

Rick A. Adams[a,*], Eduardo Aponte[a,b], Louise Marshall[a,c], Karl J. Friston[a]

[a] The Wellcome Trust Centre for Neuroimaging, Institute of Neurology, University College London, 12 Queen Square, London WC1N 3BG, UK
[b] Translational Neuromodeling Unit (TNU), Institute for Biomedical Engineering, University of Zurich & ETH Zurich, Wilfriedstr. 6, 8032 Zurich, Switzerland
[c] Sobell Department of Motor Neuroscience and Movement Disorders, UCL Institute of Neurology, 33 Queen Square, London WC1N 3BG, UK

HIGHLIGHTS

- We use a normative (Bayes optimal) model of oculomotor pursuit.
- We average the empirical responses of subjects performing a pursuit paradigm.
- We invert these responses using the pursuit model and dynamic causal modelling.
- We thereby estimate the precision of subjects' Bayesian beliefs from their pursuit.
- This could be used to quantify abnormal precision encoding in schizophrenia.

ARTICLE INFO

Article history:
Received 25 June 2014
Received in revised form
30 December 2014
Accepted 3 January 2015
Available online 10 January 2015

Keywords:
Oculomotor control
Pursuit
Active inference
Dynamic causal modelling
Precision

ABSTRACT

Background: This paper introduces a new paradigm that allows one to quantify the Bayesian beliefs evidenced by subjects during oculomotor pursuit. Subjects' eye tracking responses to a partially occluded sinusoidal target were recorded non-invasively and averaged. These response averages were then analysed using dynamic causal modelling (DCM). In DCM, observed responses are modelled using biologically plausible generative or forward models – usually biophysical models of neuronal activity.
New method: Our key innovation is to use a generative model based on a normative (Bayes-optimal) model of active inference to model oculomotor pursuit in terms of subjects' beliefs about how visual targets move and how their oculomotor system responds. Our aim here is to establish the face validity of the approach, by manipulating the content and precision of sensory information – and examining the ensuing changes in the subjects' implicit beliefs. These beliefs are inferred from their eye movements using the normative model.
Results: We show that on average, subjects respond to an increase in the 'noise' of target motion by increasing sensory precision in their models of the target trajectory. In other words, they attend more to the sensory attributes of a noisier stimulus. Conversely, subjects only change kinetic parameters in their model but not precision, in response to increased target speed.
Conclusions: Using this technique one can estimate the precisions of subjects' hierarchical Bayesian beliefs about target motion. We hope to apply this paradigm to subjects with schizophrenia, whose pursuit abnormalities may result from the abnormal encoding of precision.

1. Introduction

This paper considers the modelling of oculomotor pursuit using active inference – a normative or Bayes-optimal formulation of action and perception which has been used to address a range of issues in the cognitive neurosciences (Friston et al., 2010a). In a previous paper, we formulated oculomotor control during smooth pursuit eye movements (SPEM) in terms of active inference, with a special focus on how representations of uncertainty or precision could affect eye tracking behaviour (Adams et al., 2012). We established that impairment in the encoding of precision (inverse variance of random fluctuations) at higher levels of a hierarchical model of oculomotor control (e.g., frontal eye fields or prefrontal cortex) resulted in several SPEM abnormalities characteristic of schizophrenia; e.g., a greater slowing of pursuit during target occlusion. In this work, we use a similar generative model to predict

* Corresponding author. Tel.: +44 020 7679 9033.
E-mail address: rick.adams@ucl.ac.uk (R.A. Adams).

http://dx.doi.org/10.1016/j.jneumeth.2015.01.003

empirical eye movements, and thereby make inferences about how subjects optimise their oculomotor responses to moving targets. In particular, we were interested in whether we could induce changes in the precision subjects ascribe to sensory information (by changing the precision of target motion) and infer these subjective changes from measured eye movements.

The model of pursuit used below is based upon active inference. Active inference is a corollary of the free energy principle – a normative model of behaviour that appeals to Bayes optimality principles. In brief, the principle says that we sample sensory inputs to minimise prediction errors. Clearly, prediction errors depend upon predictions and inference about hidden states of the world causing sensory data. A crucial aspect of this inference is the proper weighting of sensory evidence and prior beliefs. Operationally, this rests upon weighting prediction errors in accord with their precision (reliability or inverse variability). This is formally identical to weighted least squares in statistics. Anecdotally, one can regard prediction errors as reporting what is newsworthy (what cannot be predicted) and precision turns up the 'volume' of processing channels with more reliable news.

In this paper, we present the methodology that enables one to quantify subjective precision on the basis of empirical eye movements – as a prelude to comparing normal and schizophrenic cohorts (see Section 3). If changes in subjective precision due to alterations in stimulus attributes can be estimated from pursuit data, then perhaps abnormalities of cortical precision found in psychiatric illness can be disclosed.

This paper comprises the following sections. Section 2.1 provides a brief introduction to active inference and predictive coding. Active inference provides a normative model of oculomotor behaviour, given a generative model that subjects used to predict their behaviour, described in Section 2.2. Section 2.3 provides a brief overview of dynamic causal modelling – a standard variational Bayesian scheme for inverting dynamic or state space models. Section 2.4 describes the experimental paradigm used to elicit oculomotor pursuit under visual occlusion and Section 3 presents the dynamic causal modelling results using the active inference model. Section 4 concludes with some comments about the potential applications of this non-invasive approach to quantifying subjective beliefs or expectations entertained by subjects – and how the scheme can be extended to cover neurophysiological responses.

2. Materials and methods

2.1. Active inference, generalised filtering and free energy

This section introduces active inference in terms of generalised Bayesian filtering – also known as predictive coding. In brief, active inference can be regarded as equipping standard Bayesian update schemes with classical reflex arcs that enable action to fulfil predictions about (hidden) states of the world. We will describe the formalism of active inference in terms of differential equations describing the dynamics of the world – and internal states of the visual–oculomotor system. This scheme is used in subsequent sections to predict pursuit movements under different levels of confidence (precision) about hierarchical predictions.

Active inference is based on three assumptions that formalise the notion that the brain generates predictions of its sensory samples to confirm hypotheses about the state of the world – and how the world is sampled:

- The brain minimises the free energy of sensory inputs defined by a generative model.

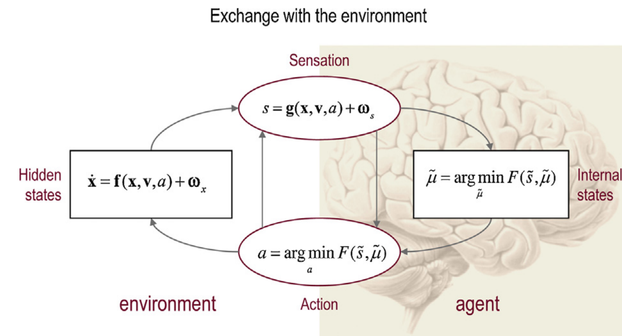

Fig. 1. Exchange with the environment. This schematic illustrates the dependencies among various quantities modelling exchanges of an agent with the environment. It shows the states of the environment and the system in terms of a probabilistic dependency graph, where connections denote directed dependencies. The quantities are described within the nodes of this graph – with exemplar forms for their dependencies on other variables (see main text). Hidden and internal states of the agent are separated by action and sensory states. Both action and internal states – encoding posterior or conditional expectations about hidden states – minimise free energy. Note that hidden states in the real world and the form of their dynamics can be different from that assumed by the generative model; this is why hidden states are in bold and internal states are in italics. See main text for further details.

- The generative model used by the brain is hierarchical, nonlinear and dynamic.
- Neuronal firing rates encode the expected state of the world, under this model.

The first assumption is the free energy principle, which leads to active inference in the embodied context of action. The free energy here is a proxy for Bayesian model evidence. In Bayesian terms, minimising free energy means that the brain maximises the evidence for its model of sensory inputs (Gregory, 1980; Ballard et al., 1983; Dayan et al., 1995; Olshausen and Field, 1996; Grossberg et al., 1997; Bialek et al., 2001; Knill and Pouget, 2004), in accord with the *Bayesian brain* hypothesis (Yuille and Kersten, 2006; Maloney and Zhang, 2010). If we also allow action to maximise model evidence we get *active inference* (Friston et al., 2010a). In this setting, desired movements are specified in terms of prior beliefs about hidden states in the generative model. Action then realises prior beliefs by sampling sensory inputs to provide evidence for those expectations. The second assumption above is motivated by noting that the world is both dynamic and nonlinear and that hierarchical structure emerges inevitably from a separation of temporal scales (Ginzburg, 1955; Haken, 1983). The final assumption is the Laplace assumption that, in terms of neural codes, leads to the *Laplace code*, which is arguably the simplest and most flexible of all candidate codes (Friston, 2009).

Under these assumptions, action and perception can be regarded as the solutions to coupled differential equations describing the dynamics of the real world, action and perception (Friston et al., 2010a):

$$\begin{aligned} s &= \mathbf{g}(\mathbf{x}, \mathbf{v}, a) + \omega_s \\ \dot{\mathbf{x}} &= \mathbf{f}(\mathbf{x}, \mathbf{v}, a) + \omega_x \end{aligned} \tag{1}$$

$$\begin{aligned} \dot{a} &= -\partial_a F(\tilde{s}, \tilde{\mu}) \\ \dot{\tilde{\mu}} &= \mathcal{D}\tilde{\mu} - \partial_{\tilde{\mu}} F(\tilde{s}, \tilde{\mu}) \end{aligned} \tag{2}$$

See Fig. 1 for a schematic summary of the conditional dependencies implied by Eqs. (1) and (2). For clarity, real-world states are written in boldface, while the states of the agent are in italics. The $\sim$ notation denotes variables in generalised coordinates of motion where $\tilde{s} = (s, s', s'', \ldots)$ (Friston et al., 2010b). The pairs of equations are coupled because sensory states $s(t)$ depend upon action $a(t)$ through non-linear functions $(\mathbf{g}, \mathbf{f})$ of hidden states and causes