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Towards a neuro-computational account of prism adaptation

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ABSTRACT

Prism adaptation has a long history as an experimental paradigm used to investigate the functional and neural processes that underlie sensorimotor control. In the neuropsychology literature, prism adaptation behaviour is typically explained by reference to a traditional cognitive psychology framework that distinguishes putative functions, such as 'strategic control' versus 'spatial realignment'. This theoretical framework lacks conceptual clarity, quantitative precision and explanatory power. Here, we advocate for an alternative computational framework that offers several advantages: 1) an algorithmic explanatory account of the computations and operations that drive behaviour; 2) expressed in quantitative mathematical terms; 3) embedded within a principled theoretical framework (Bayesian decision theory, state-space modelling); 4) that offers a means to generate and test quantitative behavioural predictions. This computational framework offers a route towards mechanistic neurocognitive explanations of prism adaptation behaviour. Thus it constitutes a conceptual advance compared to the traditional theoretical framework. In this paper, we illustrate how Bayesian decision theory and state-space models offer principled explanations for a range of behavioural phenomena in the field of prism adaptation (e.g. visual capture, magnitude of visual versus proprioceptive realignment, spontaneous recovery and dynamics of adaptation memory). We argue that this explanatory framework can advance understanding of the functional and neural mechanisms that implement prism adaptation behaviour, by enabling quantitative tests of hypotheses that go beyond merely descriptive mapping claims that 'brain area X is (somehow) *involved* in psychological process Y'.

1. Introduction

Adaptation is a fundamental property of the nervous system that enables organisms to flexibly reconfigure sensorimotor processing to counteract perturbations that cause performance errors (Shadmehr et al., 2010; Franklin and Wolpert, 2011). Consider, for example, the case of a basketball player shooting at various times throughout a game. As the game progresses, so muscles will fatigue, such that the same motor command produces a different outcome from one shoot to another. A lateral wind might also alter the trajectory of the ball and deviate it from the aimed basket. In these two situations, an internal (muscle fatigue) or external (wind) disturbance introduces systematic deviations from the intended action goal. These perturbations require the relationship between a desired action goal and the motor commands that execute it to be reconfigured, to avoid the large systematic errors in performance that would ensue if the nervous system were unable to adapt and correct for the perturbations. Thus, adaptation underwrites the maintenance of successful actions across the lifespan.

In a laboratory context, sensorimotor adaptation has been studied experimentally using a variety of methods (e.g. visuomotor rotation, force-field adaptation, saccade adaptation, Coriolis forces, etc.) (Lackner and Dizio, 1994; Shadmehr and Mussa-Ivaldi, 1994; Mazzoni and Krakauer, 2006; Ethier et al., 2008). Here we focus on a method first developed by von Helmholtz at the end of the nineteenth century, called *prism adaptation* (Von Helmholtz, 1867). In this paradigm, participants wear prism glasses that bend light, and so optically displace the visual field, for example by 10° to the right. When participants perform visuo-motor tasks (e.g. pointing at targets) while wearing the prisms, at first, they make systematic rightward errors (owing to the optical displacement), but participants learn rapidly from the error feedback to correct their movements on subsequent trials and regain normal accuracy (i.e. they adapt). When the prisms are removed post-

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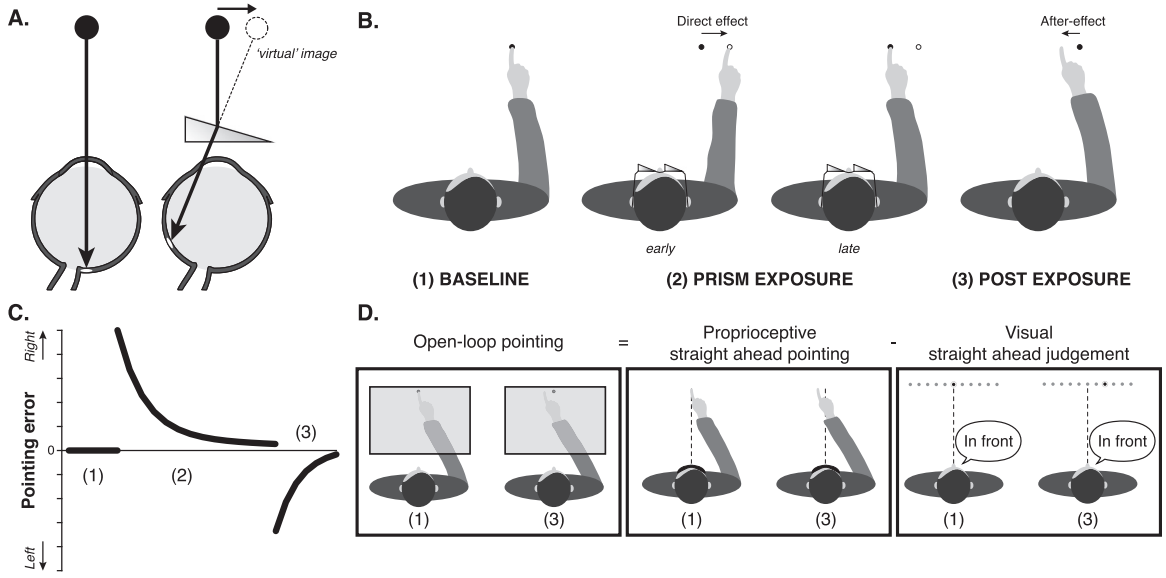

Fig. 1. Prism adaptation (A) By bending light, prism lenses displace the visual field in a direction determined by the prism structure. Here for example, light is displaced laterally, by 10° to the right. Hence, a central dot when viewed through this prism is (mis)perceived to be located 10° to the right of its true position. **(B) Typical prism adaptation experimental paradigm.** Participants' pointing accuracy is tested first at baseline (1), prior to prism exposure. Figure illustrates closed-loop pointing at baseline, i.e. participant is required to make fast and accurate pointing movements to a visual target and receives visual feedback of the reach trajectory and endpoint. During prism exposure (2), the goggles shown in A) are worn. Owing to the optical shift, the 'direct effect' is that the participant makes rightward pointing errors initially (early phase), but learns gradually from trial-by-trial error feedback to correct these errors and re-gain baseline pointing accuracy (late phase). Consequent leftward prism after-effects (errors) are measurable post-adaptation once the glasses have been removed (3). **(C) Canonical pattern of performance errors during prism adaptation**. Plot shows reach endpoint error (y-axis) as a function of trial number (x-axis) during closed-loop pointing (i.e. with visual feedback). Note baseline accuracy (i.e. mean error centred on zero) (1), followed by rightward errors (in the direction of the prismatic shift) that decrease gradually across prism exposure trials (2), followed by leftward errors (in the direction opposite the prismatic shift) after removal of the prism goggles (3). **(D) Three tests commonly used in the prism adaptation literature to quantify prism after-effects**. During *open-loop pointing* participants point at visual targets, which are viewed transiently, and visual feedback of the reach trajectory and the reach endpoint is deprived. This prevents (further) learning from endpoint error (which would over-turn the after-effect). *Open-loop pointing* measures of after-effect are deviated in the direction opposite the prismatic shift (i.e. here leftward). During *proprioceptive straight ahead pointing* blindfolded participants are asked to point in the direction they perceive as being straight ahead of their nose. This is thought to capture the proprioceptive component of adaptation. This after-effect measure is also deviated in the direction opposite to the prismatic shift (i.e. leftward). During *visual straight ahead judgement* participants must indicate when a moving light is perceived as being straight ahead of their nose. This is thought to capture the visual component of adaptation. After-effects with this measure are deviated in the same direction as the prismatic shift (i.e. rightward). The sum of visual and proprioceptive after-effects immediately after prism exposure has been shown to equal the magnitude of after-effect quantified by open-loop pointing, which is therefore known as the *total visuomotor shift* (Hay and Pick, 1966; Templeton et al., 1974; Redding and Wallace, 1988, 1996; Hatada et al., 2006a).

adaptation, individuals then make errors in the opposite direction, i.e. a leftward "after-effect", which reflects the temporary persistence of some of the compensatory mechanisms engaged during the adaptation. Several features of how prism after-effects generalise or transfer beyond the specifically trained context make it an interesting paradigm to investigate. In healthy controls, prism after-effects tend to generalise at least partially across space (Bedford, 1989, 1993; Redding and Wallace, 2006b). This contrasts with visuomotor rotation, for instance, where effects drop off sharply with distance from the trained target location (Krakauer et al., 2000). Pointing during prism exposure is typically aimed at lateral targets under speeded conditions, whereas prism after-effects are often measured at a central (untrained) location, with accuracy emphasised over speed. With this procedure, there is therefore a change in task context between prism exposure and prism after-effect measurement conditions, such that the after-effect measure intrinsically captures elements of generalisation/transfer, at least with respect to task changes (training/test or exposure/after-effect) in reach trajectory, movement speed and target location. Prism after-effects are measurable in at least three different modalities, visual, proprioceptive, and motor, which appear to follow different dynamics (Harris, 1963; Redding and Wallace, 2001; Hatada et al., 2006b, 2006c, 2006d). It has been claimed that prism after-effects can transfer to untrained visuospatial tasks (e.g. line bisection task, greyscales task), although these effects in young healthy volunteers appear to occur only with left-shifting (not right-shifting) prisms and tend to be quite small and variable (Colent et al., 2000; Michel et al., 2003; Loftus et al., 2009; Goedert et al., 2010; Martin-Arevalo et al., 2014; Schintu et al., 2014, 2017; Striemer et al., 2016). A stronger evidence base in patients has shown that the after-effects of prism adaptation can transfer to improve cognitive deficits in visuospatial neglect after right hemisphere brain damage (Rossetti et al., 1998; Frassinetti et al., 2002; Serino et al., 2009; O'Shea et al., 2017). After-effects have been shown to transfer to a broad range of untrained sensory and cognitive domains in neglect, including, for example, postural control, occulo-motor exploration, dichotic listening and mental imagery (for review, see: Jacquin-Courtois et al., 2013). Improved symptomatology after prism adaptation has also been reported in patients with complex regional pain syndrome (Sumitani et al., 2007) and Parkinson's disease (Bultitude et al., 2012). This distinctive generalisation/transfer profile of prism adaptation, by contrast with other adaptation paradigms, suggests that this experimental model of sensorimotor integration warrants special attention.

What features should a satisfying theoretical account of prism adaptation behaviour have? An ideal account would provide: 1) mechanistic explanations, that are 2) biologically plausible, and 3) can generate quantitative behavioural predictions, 4) about the effect of a range of factors, such as experimental task manipulations (e.g. modality, quality and timing of sensory feedback, gradual versus abrupt perturbation onset, etc.), psychological variables (e.g. internal state estimates of limb position, sensory uncertainty, prior knowledge of the perturbation, etc.), and neural state effects (e.g. change in neural excitability in specific brain region owing to lesion or drug or brain stimulation intervention). Here, we outline the current prevailing (descriptive psychological) model of prism adaptation that is predominant in the literature on healthy individuals, patients and animal studies. We also highlight the brain regions implicated in prism adaptation by studies conceived within this framework. Next, we make the case that a computational characterisation of prism adaptation behaviour offers advantages over this traditional functional descriptive approach, and

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