

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Special issue: Editorial

Q8 Where are we now with ‘What’ and ‘How’?

Q7 Edward de Haan ^{a,*}, Stephen R. Jackson ^b and Thomas Schenk ^c^a Department of Psychology, Amsterdam Brain and Cognition, University of Amsterdam, Amsterdam, The Netherlands^b School of Psychology, University of Nottingham, University Park, Nottingham, UK^c Ludwig-Maximilians-Universität München, Department Psychologie, Neuropsychologie, München, Germany

ARTICLE INFO

Article history:

Received 29 November 2017

Reviewed 2 December 2017

Revised 4 December 2017

Accepted 5 December 2017

Published online xxx

1. Introduction

In 1992/1995 David Milner and Mel Goodale proposed a two visual system (TVS) model that argued for the anatomical separation and functional independence of two visual processing streams: a dorsal visual processing stream associated with vision-for-action and ventral visual processing stream associated with object perception/recognition (Fig. 1). This TVS model has been, by any criteria, tremendously successful, and has inspired a considerable amount of new research, particularly with respect to the visual mechanisms and processes involved in the control of action. However, the model was very much a product of its time and pre-dated many of the techniques and methods that are now central to cognitive neuroscience (e.g., functional brain imaging). For this reason, and after 25 years, it seemed entirely sensible and appropriate to re-examine and re-evaluate the core tenets of the TVS model.

* Corresponding author. Department of Psychology, Amsterdam Brain and Cognition, University of Amsterdam, Amsterdam, The Netherlands.

E-mail addresses: E.H.F.deHaan@uva.nl (E. de Haan), Stephen.jackson@nottingham.ac.uk (S.R. Jackson), Thomas.Schenk@psy.lmu.de (T. Schenk).

<https://doi.org/10.1016/j.cortex.2017.12.001>

0010-9452/© 2017 Elsevier Ltd. All rights reserved.

During the last week of January 2016, in the middle of the skiing season, the 34th European Workshop on Cognitive Neuropsychology was held at Bressanone, Italy, during which we convened a symposium on the future of the TVS model. The discussions we had during this symposium formed the basis for this special issue of *Cortex*. The papers included in this special issue represent a mix of review articles and novel empirical studies which span monkey electrophysiology, human psychophysics, neuropsychological case and group studies, computational modelling and human brain imaging. The first paper, in which we set the stage and summarise the main observations from this special issue, was written by three of the guest editors, Edward de Haan, Stephen Jackson and Thomas Schenk. This paper is then followed by 22 papers that are either review articles, presenting a novel approach to the issues at hand, or which present original empirical evidence with respect to the TVS model. Finally, Mel Goodale and David Milner have, after 25 years, the last word.

How is the input, registered by the eyes, processed by the primate brain? Patient studies from the second half of the 19th century onwards suggested that there are a large number of visual abilities, such as the recognition of colour (Zeki & Marini, 1998), motion (Zihl, Von Cramon, & Mai, 1983), or faces (Bodamer, 1947), that can be impaired in isolation, and therefore, may be represented separately within the brain. Next, the functional architecture of the primate brain was explored in detail in animal studies using research methodologies such as staining, tracing and electrophysiology (Livingstone & Hubel, 1988). Based on these studies, an architecture was gradually uncovered, consisting of many separate retinotopic maps whose contribution to visual

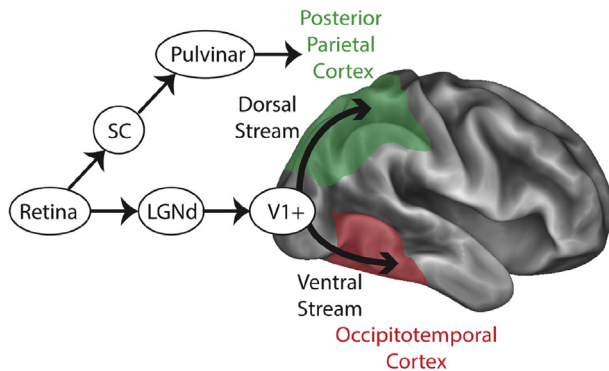


Fig. 1 – The model of Goodale and Milner (1992).

processing appeared to be dominated by one aspect of the outside of the world, such as colour, form, motion, or location (see again: Livingstone & Hubel, 1988). This constellation of multiple, dedicated maps was subsequently confirmed in the human brain by neuroanatomists (e.g. Bourne, 2010) and functional neuroimaging (e.g. McKeefry et al., 2009; Vasseur et al., 2010). There is now evidence for more than 40 separate visual maps in the posterior brain (Tootell, Tsao, & Vanduffel, 2003; Van Essen, 2005).

In order to understand this fractionated architecture, the concept of cortical ‘pathways’ was introduced. Ingle (1967) and Schneider (1967) were among the first to suggest that there might be different pathways for what and where. They suggested that visual processing was segregated into a sub-cortical pathway to the mid-brain, dealing with localisation of stimuli and their orientation, and a single cortical pathway dealing with the identification of the same stimuli. In 1969, Newcombe (1969) observed in her sample of second world war patients with gunshot wounds that a subgroup with parietal lobe lesions performed poorly on tasks that required visuo-spatial perception (e.g., maze learning) even though their performance on visual recognition tasks, e.g. Mooney faces test, was normal. In contrast, a subgroup of patients with temporal lobe damage showed the reverse pattern. This observation was confirmed and subsequently investigated in detail by Ungerleider and Mishkin (1982) in a series of influential lesion studies in macaque monkeys. The monkeys were impaired on a landmark task after a parietal lesion and on a recognition task after a temporal lesion. Ungerleider and Mishkin were the first to suggest that these different maps were not randomly sprinkled over the visual cortex but were instead organised into two major pathways, each arising from the primary visual cortex, V1. The first, known as the ‘where-pathway’, spreads from V1 dorsally to the parietal lobe. The maps that together constitute this dorsal pathway, process different aspects of the spatial layout of the outside world, such as location, distance, relative position, position in egocentric space, and motion. The second, ventral, route was referred to as the ‘what-pathway’, and the apparent serial processing in the sequence of maps allows us to perceive and recognise shape, orientation, size, objects, faces, and text. This view was then subsequently refined by Goodale and Milner (1992) who argued that the concept of these two pathways should not so much be framed in terms of two

different perceptual processing streams based upon different input, but rather, in terms of what the visual information was used for. Fig. 1 shows a schematic representation of the Milner and Goodale model of two major pathways, each arising from the primary visual cortex, V1. The first, now renamed as the ‘how-pathway’, spreads from V1 dorsally to the parietal lobe. The second, ventral route continues to be named ‘what-pathway’. The visual information in the ventral stream terminates in the medial temporal lobe, hippocampus and amygdala and is used for visual recognition and memory and emotional content, while the dorsal route processes visual information for action and feeds into the motor cortex of the frontal lobe.

This TVS model, proposed by Milner and Goodale in 1992/1995, and subsequently revised in several publications (e.g. Goodale, 2010; Milner & Goodale, 2008) since, provided an elegant description of a large body of empirical data, proved to be a catalyst for a very large number of studies (Fig. 2), and a useful heuristic for thinking about visual perception and perceptual processing more widely [Note: the TVS model subsequently served as an inspiration for similar models for both auditory (Zatorre et al., 2007) and somatosensory processing (Dijkerman & de Haan, 2007)].

Arguably, the immediate appeal of the TVS model resulted from its clear statement of a number of attractive core ideas, and from the presentation of some remarkable neuropsychological evidence in support of these ideas – most notably that obtained from studying the patient DF. These core ideas were as follows: First, that there was a clear *anatomical separation* of the dorsal and ventral visual processing pathways in the brain: one for action and the other for perception. Second, that the nature of these two pathways was determined not by the type of inputs that they received (i.e., object-based versus spatial information), but rather *by how this information was to be used*, e.g., spatial information used for object recognition versus spatial information used for visually guided action. Third, that the dorsal and ventral visual processing pathways were *functionally independent* of one another. Importantly, for this idea of functional independent processing to be at all meaningful, it suggests that there can be no, or very little, *cross-talk* between the two pathways. Fourth, that the processing in the ventral pathway may lead to a *conscious percept* but there is no introspection possible for the processing within the dorsal route. Finally, although there are many recurrent processing loops within each pathway, a key suggestion is that there is a *linear, hierarchical relationship* between the posterior to anterior processing stages in each case.

While having broad appeal, some aspects of the TVS model began to be challenged even quite soon after the publication of the complete TVS account in 1995 (e.g. Brenner & Smeets, 1996; Jackson & Shaw, 2000), and since that time, a growing number of objections to the original TVS model have been raised (e.g. Jeannerod & Jacob, 2005; Rizzolatti & Matelli, 2003; Rossetti, Pisella, & Vighetto, 2003; Schenk & McIntosh, 2010; Schenk, 2010; Singh-Curry & Husain, 2009; De Haan & Cowey, 2011). For this reason we felt that it was time to both recognise the enormous contribution of the TVS model and to consider its current status. The Bressanone symposium was a first step in this process of taking stock. The main issue considered was which aspects of the model had stood the test

Download English Version:

<https://daneshyari.com/en/article/7312094>

Download Persian Version:

<https://daneshyari.com/article/7312094>

[Daneshyari.com](https://daneshyari.com)