



## Special issue: Editorial

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

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## ARTICLE INFO

## Article history:

Received 29 November 2017

Reviewed 2 December 2017

Revised 4 December 2017

Accepted 5 December 2017

Published online 13 December 2017

## 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 a 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.

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.

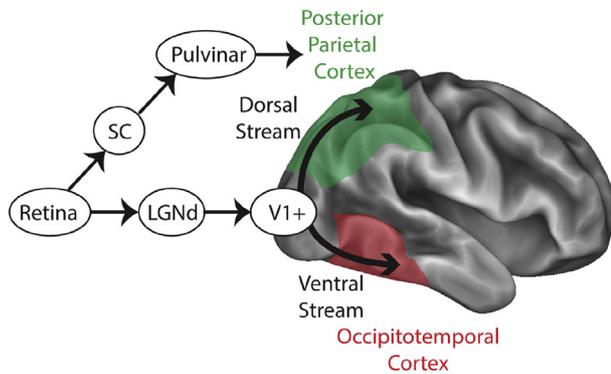
How is the input, registered by the eyes, processed by the primate brain? Patient studies from the second half of the 19th century onwards suggested that there are a large number of visual abilities, such as the recognition of colour (Zeki & Marini, 1998), motion (Zihl, Von Cramon, & Mai, 1983), or faces (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

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

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**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, Gouws, Burton, & Morland, 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.<sup>1</sup>

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

<sup>1</sup> Note: the TVS model subsequently served as an inspiration for similar models for both auditory (Zatorre, Chen, & Penhune, 2007) and somatosensory processing (Dijkerman & de Haan, 2007).

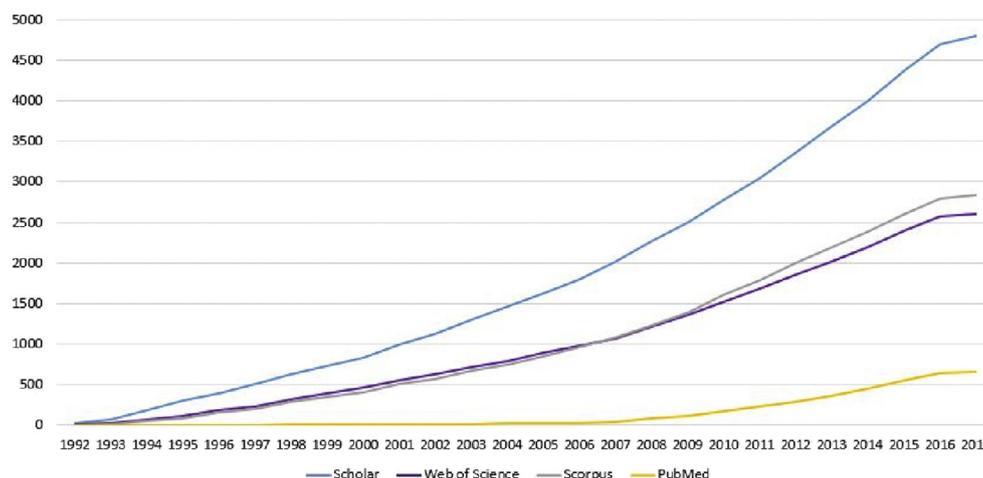


Fig. 2 – The number of publications citing the Goodale & Milner TVS model from 1992 until 2017.

first step in this process of taking stock. The main issue considered was which aspects of the model had stood the test of time, and which aspects were in need of revision. This special issue is the next step in the process. In this introductory paper, we present an overview of the papers that are collated in this special issue, using the core ideas referred to above as the organising principle.

### 1.1. Anatomical separation (two pathways for perception and action) and functional independence

The original TVS model can be seen to be very much a product of its time, and of the research methods that were at the forefront in guiding our thinking in the 1980s and early 1990s. These methods included: electrophysiology studies of the monkey brain; behavioural and psychophysical studies of human perception and action; and most notably, neuropsychological studies of brain injured patients or groups of patients that placed considerable emphasis on the demonstration of single or double dissociations between patterns of spared or impaired function. Such dissociations included the finding that a patient with severe visual form agnosia (DF), who presented with profound difficulties in object recognition and perception, could nonetheless, and quite remarkably, reach accurately and orient her hand appropriately when executing visually guided movements toward a visual object (Milner & Goodale, 1995). It is no surprise therefore that based upon such demonstrations (and many others), the TVS model should stress the anatomical separation and functional independence of the ventral (object-perception) and dorsal (visually guided action) visual processing streams. This special issue of *Cortex* contains a number of papers that utilize or discuss data based upon these same methods of monkey electrophysiology (e.g., Galletti & Fattori), behavioural and psychophysical studies of human perception and action (e.g., Whitwell, Goodale, Merritt, & Enns; De la Mala, Smeets, & Brenner; Medendorp, De Brouwer, & Smeets; Namdar, Algom, & Ganel; Schenk, Hesse, & Billino; and Rauschecker), and neuropsychological studies of brain-injured patients or groups of patients (e.g., Bartolo et al.; Rossitt et al.; Jackson

et al.; Renning, Karnath, Cornelissen, Wilhelm & Himmelbach; Utz et al.; and Ross, Schenk, Billino, Macleod, & Hesse). While some of these papers provide support for the original conceptualisation of the TVS model; for the most part they call into question many of the core ideas outlined in the TVS model, and argue against any simple distinction based upon anatomical separation and functional independence of vision for perception and vision for action.

One of the most obvious and important methodological developments that has taken place since the late 1980s and early 1990s has been the development of functional brain imaging; with its particular emphasis on whole-brain analyses of perceptual, motor and cognitive function, and more recently with the development of techniques for investigating brain connectivity and functional brain networks. Another important methodological development has been the increased use of computational modelling approaches to understand brain function and model brain networks. The use of these techniques has resulted in a substantive shift in focus away from a modular view of the brain, and toward a vision of brain function that emphasises the dynamic, flexible, and context-dependent, operation of brain networks. This special issue contains a number of papers that report either brain imaging studies of perception and/or action (e.g., Cavina-Pratesi et al.; Freud et al.; Haak & Beckman; and Hutchison & Gallivan) or computational studies (e.g., Scholte, Losch, Ramakrishnan, De Haan, & Bohte). For the most part these studies argue for: an increased complexity of the functional anatomy of object representations or visually guided action; an increased number of visual processing streams; or a set of highly interactive brain areas that can combine flexibly and dynamically according to different task demands.

From its earliest days, one of the most hotly contested aspects of the TVS model has been the suggestion that the dorsal stream mechanisms responsible for the visual control of action were substantially less susceptible to the influence of pictorial illusions than the ventral stream object recognition mechanisms (e.g., Aglioti, De Souza, & Goodale, 1995; Brenner & Smeets, 1996; Jackson & Shaw, 2000; Koppiske, Bruno, Hesse, Schenk, & Franz, 2016), and this debate continues in this

special issue. [Whitwell et al.](#) report a study in which research participants either reached out to pick up 3D target bars that were resting upon a picture of the Sander's Parallelogram illusion, or made explicit estimates of the length of the 3D bars. Consistent with previous studies they report that the effects of the illusion are stronger for perceptual judgements than for grasping movements. [Namdar et al.](#) also report a psychophysical investigation of perceptual judgement and grasping movements in the same individuals. Specifically, they investigate a phenomenon that they have called the Range of Standards Effect and demonstrate that this effect is limited to perceptual estimation and does not extend to grasping actions. Consistent with the TVS model, they argue that visual perception and visually guided action are governed by separate rules and mediated by different mechanisms.

By contrast, [De la Malla et al.](#) investigated the effect of a visual illusion on both perceptual judgements and visually guided action. They had participants intercept a moving object (a Gabor patch) that appears to move at a different speed than its true speed due to the effect of an illusion. They used two-interval forced choice discrimination tasks to determine how the moving grating influenced people's judgments of the object's position and velocity while they were fixating, and demonstrated that individual errors in perceptual judgement closely matched the errors that subjects made when trying to intercept the targets. The authors argue that this finding does not support the TVS model. Similarly, [Medendorp et al.](#) review their recent behavioural and brain imaging studies of single and double saccade paradigms. They describe results showing that the presentation time of the illusion affects both saccade amplitude and perceptual judgments in a similar way, and that visuomotor updating is also affected by illusory context. Based upon these findings they argue for a common, dynamic, visual representation that drives both perception and action, or that there is no absolute functional specialization of the two visual processing streams.

In their paper, [Schenk & Hesse](#) also reflect upon the role of visual memory in action control and focus in particular on the proposal that visual information from the dorsal system cannot guide actions that are based on memorized visual information, which they colourfully refer to as the dorsal amnesia hypothesis. After conducting a wide-ranging review of the evidence [Schenk & Hesse](#) conclude that the dorsal amnesia hypothesis is no longer tenable. Finally, Josef Rauschecker reports a review of the auditory system and cites evidence in support of the dual-system viewpoint.

### 1.2. Re-examining the neuropsychological evidence for anatomically separate and functionally independent visual processing streams

As was noted above, much of the widespread initial appeal of the TVS model came from the remarkable demonstration of dissociations between patterns of spared or impaired function in neuropsychological patients, such as the visual form agnostic patient DF and patients presenting with optic ataxia following dorsal stream damage. In fact, the contrast between preserved visually guided action and impaired visual object perception in patient DF and between impaired visually guided reaching and preserved visual perception in optic

ataxia can be very clearly viewed as the cornerstone of the TVS model. In many of the papers reported in this special issue the neuropsychological evidence in support of the TVS model is re-examined in the light of new or conflicting evidence.

[Rossitt et al.](#) report an interesting set of findings with respect to the visually guided reaching movements of the visual form agnostic patient DF. Recall that DF, in spite of her profound inability to identify and distinguish visual stimuli, was reported to be able to use visual information to control her hand actions towards these same stimuli, and these observations were cited as the basis for a double dissociation with optic ataxia. In their new study [Rossitt et al.](#) investigated DF's reaching abilities for targets presented in central (foveated) and peripheral (extra-foveal) vision, and demonstrate that DF is highly inaccurate when reaching to extra-foveal visual targets, and thus follows the pattern seen in optic ataxic patients. The authors conclude that their findings call into question the long-standing assumption that DF's dorsal visual stream is functionally intact, and they conclude that patient DF can no longer be considered as an appropriate single-case model for testing the neural basis of perception and action dissociations. Similar findings were reported by [Hesse, Ball and Schenk \(2012, 2014\)](#).

Conversely, both [Bartolo et al.](#) and [Jackson et al.](#) examine perceptual processing impairments in patients with optic ataxia. First, [Rossetti et al.](#) investigated whether the processing of target locations for action also has an effect on the representation of peripersonal space. They examined judgements of hand-to-target distances in the optic ataxic patient IG and demonstrated specific difficulties in processing hand-to-target distances in a motor task and also in a perceptual judgement task requiring identification of what is reachable within the visual environment. They also demonstrated that these perceptual difficulties are especially evident when both the target and the hand are perceived in the visual periphery. Similarly, [Jackson et al.](#) examined visual and non-visual perception in optic ataxic patients using a bimanual haptic matching task that was performed without vision, where the bar to be matched was presented haptically or visually. They demonstrated that, unlike neurologically healthy controls who could all perform this task with high levels of accuracy, none of the optic ataxic patients were able to perform the task. The authors conclude that optic ataxic patients may exhibit an impairment across a range of behavioural tasks, including visually guided reaching, that is characterised by an inability to simultaneously and directly compare two spatial representations.

In their paper, [Utz et al.](#) report an investigation of visually guided reaching movements in a large ( $n = 43$ ) group of right brain-damaged individuals with and without neglect, and a group of healthy controls, on a pro- and anti-pointing task. Specifically, they examine the effects of providing or withdrawing visual feedback on pro- and anti-pointing and demonstrate that withdrawal of visual feedback has a stronger effect on pro-pointing compared to anti-pointing, and that this effect is stronger in neglect patients compared to patients without neglect or controls. By contrast, [Himmelbach et al.](#) examine a group of patients with object recognition difficulties. They present objects for recognition within the lateral

visual field and report that while object recognition for stimuli presented in the contralesional visual field is impaired, object recognition for objects presented in the ipsilesional hemifield is intact. They argue that the object recognition system needs two intact ventral pathways for object recognition across the whole visual field.

As noted above, another of the core ideas associated with the TVS model has been the association of conscious awareness with visual processing in the ventral stream but not the dorsal stream. One line of evidence that contributed to this viewpoint were reports of ‘Action-blindsight’ - the demonstration that cortically blind individuals were able to successfully avoid an obstacle placed within their blind field, despite reporting no conscious awareness of that obstacle. [Ross et al.](#) re-examined this phenomenon in a group of 6 patients with highly circumscribed lesions in the occipital lobe (including V1) that spared the subcortical structures associated with Action-blindsight. They demonstrate that none of the patients showed reliable avoidance behaviour and conclude that obstacle avoidance likely relies upon visual input from occipital cortex. This paper is accompanied by a pair of articles that discuss the implications of the paper by Ross and colleagues ([Striemer, Chapman, & Goodale](#) and [Hesse, Billino & Schenk](#)).

Taken together, the neuropsychological studies reported within this special issue indicate that the simple story of a clear anatomical separation and functional independence of vision for action and vision for perception, based upon the double dissociation of visual form agnosia and optic ataxia, can no longer be sustained. Instead, recent evidence indicates that neuropsychological patients invariably present with impairments that impact on both perception and action and thus provide little support for strong claims of anatomical separation and functional independence outlined in the initial TVS model.

### 1.3. Neuroimaging studies of visual perception and the visual control of action

In their paper, [Cavina-Pratesi](#) and colleagues use functional brain imaging techniques to investigate the neural basis for visually guided grasping, reaching and pointing movements ([Cavina-Pratesi et al.](#)). Using a subtractive logic they demonstrate that there are widespread brain activations associated with these tasks, but that these activations are subtly different according to task context, including the potential communicative requirements of the task. [Freud et al.](#) reach a similar conclusion in their paper. They used fMRI together with multivariate analysis methods (Multivoxel Pattern Analysis - MVPA) to compare patterns of activation for reaching and grasping movements directed to real objects or 2D images. Their results also indicate that the brain response observed differs according to task context, i.e. reach vs. grasp response and real vs. 2D object.

### 1.4. Are there more than two visual processing streams?

[Haak & Beckman](#) report a resting-state fMRI study in which they estimated the functional connectivity patterns between 22 human visual areas using a dataset from 470 individuals.

They report that an objective, data-driven, analysis of the topological organisation of connectivity reveals a highly significant triple dissociation between the retinotopic areas on the dorsal, ventral and lateral surfaces of the human occipital lobe. They suggest that the functional organisation of the human visual system involves not two but three cortical pathways.

### 1.5. Cross-talk between the two visual streams

In their paper, [Janssen, Behoef, & Premereur](#) review evidence from anatomy, modelling, electrophysiology, electrical stimulation, reversible inactivation, and functional imaging in the macaque monkey aimed at clarifying at which levels in the hierarchy of visual areas the two visual streams interact. They argue that neurons in both streams encode 3D structure from binocular disparity and that synchronized activity between parietal and infero-temporal areas is present during 3D structure categorization, and clusters of 3D structure-selective neurons in parietal cortex are anatomically connected to ventral stream areas. They propose that both anatomical and functional evidence indicate that the dorsal and the ventral visual stream interact during the viewing of 3D objects.

Similarly, [Galletti & Fattori](#) review evidence from studies of the monkey and human brain in support of the viewpoint that information regarding visual motion flows along two different paths within the dorsal visual processing stream: a dorsolateral path that flows towards areas MT/V5, MST, V3A, and a dorsomedial one that flows towards the visuomotor areas of the superior parietal lobule (V6A, MIP, VIP). The authors note that these dorsolateral and dorsomedial streams represent only two examples and that many other streams have been described. They propose that such cortical streams should not be viewed as fixed sets of interconnected cortical areas in which each area belongs unequivocally to one stream and is involved in only one function. Instead they argue for interconnected neuronal networks, often involving the same neurons, that are involved in a number of functional processes and whose activation changes dynamically according to context.

[Scholte et al.](#) use a computational modelling approach to understand why there might be multiple visual processing pathways. Specifically, they used deep neural networks (DNNs) that learn from data based upon the optimization of cost functions that map the state of the system to a measure of performance. This results in a network with units in which the lower layers of the network are tuned to the statistical structure of the input while higher layers are tuned to the cost function used for training the task. The authors argue that tasks become easier to solve when they are decomposed into subtasks with their own, uncorrelated, cost function, and “vision for perception” and “vision for action” are examples of such a decomposition. They predict that the degree to which cost-functions correlate is a good descriptor of the degree to which the tasks associated with the cost-function will share cortical units.

[Hutchison & Gallivan](#) also used fMRI and functional connectivity analyses in their study to examine interactions between regions of fronto-parietal cortex associated with vision-for-action and regions of occipito-temporal cortex associated with visual perception and object recognition. Their findings

indicate that the functional coupling between ventral-lateral areas of the occipito-temporal cortex and dorsal parietal and ventral-medial structures is flexible and task-dependent. The authors propose that regions in lateral occipital cortex may play an important role in mediating interactions between the dorsal and ventral pathways during sensorimotor tasks.

The papers reported above have used modern computational modelling techniques and/or brain imaging and functional connectivity methods to re-examine the core claim of the TVS model: that vision-for-action and visual perception/object recognition can be separated into two anatomically separate and functionally independent visual processing streams. Together the findings of these studies provide little support for the key claim of the TVS model. Instead, the studies argue for more than two streams, or, more importantly, for a flexible and dynamic pattern of interaction between visual processing areas in which visually processing networks may be created on-the-fly in a highly task-specific manner. While it might be argued that the original TVS model allowed for some cross-talk between the dorsal and ventral streams, it becomes somewhat meaningless to continue to argue for functionally independent visual processing systems when the prevailing evidence suggests that cross-talk is the norm rather than the exception.

In summary, the TVS model proposed by David Milner and Mel Goodale in the early 1990s has been tremendously successful in driving forward our understanding of the visual brain and visually guided behaviour. The model, when it first appeared, was bold and exciting and 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 such as computer-intensive modelling, brain imaging, and connectomics that have now come to the forefront of our field. 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. The 22 papers presented within this special issue of *Cortex* contain a mix of review articles and novel empirical studies that span monkey electrophysiology, human psychophysics, neuropsychological case and group studies, computational modelling and human brain imaging studies. Together they provide a comprehensive review of the current state-of-the-art which will allow the reader to form an opinion on the continuing importance of the TVS model.

## Acknowledgements

Edward de Haan is supported by ERC grant FAB4V (#339374). The authors would like to thank Katherine Dyke for creating Figure 2.

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