

Contents lists available at ScienceDirect

Vision Research

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

Review

Visuomotor robustness is based on integration not segregation

Thomas Schenk

Cognitive Neuroscience Research Unit, Wolfson Research Institute, University of Durham, Queen's Campus, University Boulevard, Thornaby, Stockton-on-Tees, TS17 6BH, UK

ARTICLE INFO

Article history:

Received 16 June 2010

Received in revised form 9 August 2010

Keywords:

Perception–action

Dorsal–ventral

Cue–reliability

Visual form agnosia

Sensorimotor control

ABSTRACT

How can we explain, that DF – a patient with a damaged ventral stream – can act normally in many everyday tasks despite her profound perceptual disability. The classical answer is that perception and action are based on separate visual streams. Here, I will explain why this view is problematic and offer an alternative answer. Specifically, I will argue that the preserved performance of DF should be seen as evidence of the redundancy of visuomotor control and not as evidence of a segregation between vision for perception and action.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

In 1991 Goodale, Milner and their colleagues reported the case of DF, a patient with a severe form of visual form agnosia. DF was surprisingly adept at using visual information to guide her actions despite her profound perceptual difficulties (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). These perceptual deficits were caused by bilateral lesions to the lateral surface of the posterior aspects of the temporal cortex (James, Culham, Humphrey, Milner, & Goodale, 2003; Milner et al., 1991). The observations in DF were related to a well-known distinction between the ventral and dorsal visual streams of the primate visual cortex. According to this classification the ventral stream consists of areas in the occipito-temporal and temporal cortex and the dorsal stream comprises areas in the occipito-parietal and parietal cortex (Ungerleider & Haxby, 1994; Ungerleider & Mishkin, 1982). It was argued that DF's lesions effectively disconnected her ventral stream from visual input (Milner et al., 1991). Her preserved visuomotor abilities were thus regarded as evidence that the ventral stream plays no direct role in the visual control of movements giving rise to the perception/action model (Milner & Goodale, 1995, 2006). The central claim of this model is that the two visual streams serve distinct behavioural roles. The ventral stream provides vision for perception, is connected to neural structures related to memory and cognition and only plays an indirect role in the visual guidance of action. In contrast the dorsal visual stream has direct links with the motor cortex and is thus directly involved in the control of action. In a recent discussion paper we examined the evidence for and against the perception/action model. We con-

cluded, that the core assumption of the perception/action model of two independent visual streams serving two distinct behavioural purposes has become difficult to maintain in the face of recent evidence (Schenk & McIntosh, 2010). Instead we suggested that for most examples of visuomotor behaviour input from both the dorsal and ventral streams will be combined. In their reply Goodale and Milner (2010) challenged this conclusion and argued that our view is incompatible with the remarkable range of normal visuomotor performance found in the visual form agnostic patient DF.

In this article I will examine this challenge. For this purpose I distinguish between two possible accounts of visuomotor control: the segregation and the *integration* account. The segregation-account assumes that the two visual streams serve different behavioural roles. It is assumed that only one of them, the dorsal stream, is directly involved in the control of action. In contrast the integration account assumes that both streams are directly involved in the control of action.

My aim is to show that an integration account of visuomotor control is in fact compatible with DF's visuomotor behaviour and can account better for findings obtained in healthy participants. However, before I can present the case for the integration account I should first justify why I think the segregation account is unsatisfactory. This will be done in the following section.

2. Is the ventral system only indirectly involved in action?

To see whether the segregation account can explain the pattern of preserved and impaired behaviour found in DF it is crucial that we understand which aspects of behaviour are supposedly served by the ventral and the dorsal visual streams. A superficial understanding of the perception/action model suggests a very simple an-

E-mail address: thomas.schenk@dur.ac.uk

swer: the visual guidance of action is the domain of the dorsal stream and the ventral stream is only involved in perceptual tasks. However, this view is wrong and Milner and Goodale (1995, 2006, 2008) consistently stressed that the ventral stream does play a role in the visual control in action albeit an indirect one.

This distinction between a direct versus an indirect role in the visual control of action is somewhat fuzzy. Milner, Goodale and colleagues (Dijkerman, McIntosh, Schindler, Nijboer, & Milner, 2009; Goodale & Milner, 2010; Milner & Goodale, 1995, 2006, 2008) use the well-known distinction between motor-programming and motor planning to make the distinction between *direct* and *indirect* visual control of action clearer. In the following I will therefore introduce and discuss the programming-planning distinction. But first I should clarify how in the perception–action model the distinctions of direct versus indirect control, programming versus planning and ventral versus dorsal streams relate to each other. A direct role of vision in action control means that vision contributes to the programming of specific actions. The meaning of indirect control is less well-defined. Motor planning is one example of indirect control, but not necessarily the only one. Another example is visual attention. Visual processes involved in guiding our attention can make the observer aware of the need to produce a motor response without necessarily providing the specific information that will shape that response. In this sense visual processes involved in attention are also seen as processes which may only indirectly influence action (Milner & Goodale, 1995, Chapter 7). How does this distinction between direct and indirect control of action map onto the ventral–dorsal distinction? According to the perception–action model only the dorsal stream can support direct visual control of action. This means the dorsal stream can be involved in motor programming and planning, but the ventral stream can only be involved in motor planning but not in motor programming. However, such a claim is only useful if we have reliable criteria to distinguish between programming and planning. Do we have such criteria? In the next paragraphs I will first describe the origin of the programming-planning distinction before I discuss whether reliable criteria for this distinction can be found.

The distinction between motor programming and planning goes back to Schmidt's (1975) motor schema theory. The core concept in this theory is the motor schema: a template for carrying out specific motor skills which retains sufficient flexibility to account for our ability to execute the same skill under varying circumstances. A typical example is the writing of letters. Once we learned to write a specific letter, we can do that on vastly different spatial scales, with different writing utensils and different effectors (Plamondon, Stelmach, & Teasdale, 1990; Stelmach, Mullins, & Teulings, 1984). Such variations like spatial scale, employed tool or effector are seen as parameters of the schema. These parameters have to be specified before an executable motor program is created. This process of parameter-specification is called motor programming and it is distinguished from motor planning – the selection of different motor schemas.

Milner and Goodale's (1995, 2006, 2008) definitions of these concepts are similar, although their definitions have a more physiological flavour. They assume that visuomotor control employs a collection of specialized visuomotor circuits which we inherited from more primitive animals. These visuomotor circuits are defined by pre-determined sensory/input-channels linked to specific motor/output channels. Although these input–output mappings are fixed and define a given visuomotor circuit, they can be adapted to specific motor tasks. For example, we might have a circuit for grasping movements, but the grasping movements will need to be modified to take account of the size and form of the object and the distance between hand and object. These circuits can be seen as pre-defined programs containing motor variables that

are adjustable on the basis of sensory input. These adjustments are called motor programming. In contrast, the process of selecting a circuit or combination of circuits for a specific behavioural goal is called motor planning. Replace the terms “visuomotor circuit” with “motor schema” and the definitions for motor programming and planning in the perception–action model become the same as those in Schmidt's (1975) motor schema theory.

Schmidt's motor schema theory is therefore a good place to look for clear criteria distinguishing motor programming and planning. Unfortunately, it is exactly the absence of such criteria which in recent reviews of the motor schema theory has been identified as its main flaw (Alexander, Delong, & Crutcher, 1992; Shaffer, 1992). This is also a problem for the perception/action model. Without such criteria we cannot decide whether a failure by DF to perform a given visuomotor task should be regarded as a planning error (as expected by the perception/action model) or a programming error. But why is it so difficult to distinguish between programming and planning errors? Let us assume that to pick up a specific object DF uses an abnormal grasp. Is this a programming error or a planning error? According to the motor schema theory the answer has to be the following: If DF's grasp and the normal grasp correspond to different motor schemas, DF's error is a failure in selecting the correct schema and is therefore a planning error. If however, the incorrect and normal grasps are variations of the same motor schema, the error is a failure to determine the correct value for the relevant parameter of the motor schema and is thus a programming error. This distinction is easy to make at a theoretical level, but very difficult to make in practice. Such a decision requires that we know which movements (or in our example which grasps) are variations of the same motor schema or expressions of two distinct schemas. This knowledge is, however, not available. Given that researchers cannot even agree whether motor schemas exist (Summers & Anson, 2009), even less agreement should be expected when it comes to decide whether two movements or skills belong to the same or different schemas.

Dijkerman et al. (2009) tried to address this problem by providing their own criteria. Motor planning involves the selection of higher-order aspects of movements such as the type of grasp or the hand to be used. In contrast, motor programming relates to movement parameters that bear a direct relation to the relevant visual characteristic of the visuomotor task. A typical example for the latter would be the specification of the size of hand-opening as determined by the size of the object. But does this definition help? Their motor planning definition is not more specific than the one which we already had. Their definition of motor programming is more specific, but difficult to apply to individual actions. To determine whether the relation between relevant visual characteristics and relevant movement parameters corresponds to “a relatively direct translation” we need to know the relevant visual characteristics of the task and the parameters of the movement. This may appear very clear in a given example (e.g. grasping: object size and hand-opening). But this clarity reflects more our lack of imagination than any form of knowledge. In fact it turns out that the relationship between visual and movement parameters depends on how you analyse a specific visuomotor task.

Let's take the example of reaching or pointing. One possible way of analysing this task would suggest that the relevant visual parameter is the perceived distance between observer and target and the relevant motor parameter is the required movement amplitude (i.e. distance between the hand's start and end position). In this case the relationship between visual and movement parameters is direct and simple. But we would be equally justified in assuming that the relevant “motor parameters” are the joints contributing to the movement and the degree of joint extensions needed to transform the starting posture into the required final posture. If we adopt the latter description – (a position favoured

by many current motor control researchers: [Diedrichsen, Shadmehr, & Ivry, 2009](#); [Todorov, 2004](#); [Wolpert & Ghahramani, 2000](#)) a mapping of visual distance onto required joint movements is required. Such a mapping is certainly not direct and simple. Thus, to apply the criteria suggested by [Dijkerman et al. \(2009\)](#) we need to know which parameters the brain uses for a given visuomotor task. However, in many cases this is not known or as in the case of grasping is the subject of controversy ([Hoff & Arbib, 1993](#); [Smeets & Brenner, 1999](#)).

Moreover, if we hoped that electrophysiological recordings from the motor cortex might provide the answer, we will again be disappointed. Early electrophysiological recordings from monkeys suggested that at the population level such “high level” movement parameters as movement direction are encoded in the motor cortex ([Georgopoulos, Kalaska, Caminiti, & Massey, 1982](#)). But this claim is now disputed by [Todorov \(2000a\)](#). In Todorov’s model the motor cortex codes low-level aspects of the movement, namely muscle group activations. [Todorov \(2000a\)](#) argues that earlier interpretations of the signals from the motor cortex did not take into consideration the state-dependence of muscle-force production and multi-joint mechanics. If this is taken into account, cortical signals for the activation of specific muscle groups will be correlated with “high level” movement kinematics. This means that correlations between single-unit recordings and high-level kinematics cannot be taken as evidence for the representation of high-level features at the level of the motor cortex. In fact [Todorov \(2000a\)](#) showed that a model based on low-level movement features cannot only account for the observed correlation with high-level kinematics, but also account for some otherwise difficult to explain electrophysiological findings (for an interesting discussion of these claims, see: [Georgopoulos & Ashe, 2000](#); [Moran & Schwartz, 2000](#); [Scott, 2000a, 2000b](#); [Todorov, 2000b](#)). Thus, neither models of motor control nor neurophysiological data allow us to identify the relevant visual and motor parameters. Without this knowledge it is impossible to say whether a given visuo-to-motor mapping corresponds to a “direct translation” and thus impossible to apply [Dijkerman et al.’s \(2009\)](#) definition of motor programming.

But it is not just the specific distinction between programming and planning which falls short of providing a convincing explanation for DF’s visuomotor behaviour. It also seems unlikely that any other motor-based criteria will fare any better. For example DF shows normal grip-point selection when picking up ellipsoid objects ([Goodale, Meenan et al., 1994c](#)) but falters when picking up cross-shaped objects ([Carey, Harvey, & Milner, 1996](#)). Similarly she shows normal posting behaviour for a simple rectangular card ([Milner et al., 1991](#)), but is impaired when posting a T-shaped object ([Goodale, Jakobson et al., 1994b](#)). It seems that visual rather than motor demands determine the ventral stream’s involvement in visuomotor control and this is best shown by studies examining the role of depth cues in reaching. DF’s reaching and grasping behaviour diverges significantly from normal performance when binocular and extraretinal depth-cues are distorted or removed ([Carey, Dijkerman, & Milner, 1998](#); [Dijkerman, Milner, & Carey, 1996, 1999](#); [Marotta, Behrmann, & Goodale, 1997](#); [Mon-Williams, Tresilian, McIntosh, & Milner, 2001b](#)). It appears that the ventral stream is not needed for reaching when binocular and extraretinal cues are available, but in their absence an intact ventral stream becomes essential for normal visuomotor performance.

I have tried to show that the distinction between direct and indirect visual control of action and the associated dichotomy between motor programming and planning are problematic. One problem is that it is difficult to apply those dichotomies to concrete examples of visuomotor behaviour. This in turn makes it difficult to use those distinctions to predict when the ventral stream will become involved in visuomotor behaviour. Moreover, looking at DF’s behaviour it appears that the two visual streams differ primar-

ily in terms of the sensory information they can provide rather than in terms of the motor behaviour they control.

Thus with respect to its role in the control of movement the two visual streams do not seem to be categorically different. But this similarity does not mean the dorsal and ventral stream’s contribution to visuomotor behaviour is equal. Evidence from functional imaging suggests that the dorsal system is more specialized for visuomotor control than the ventral system. A number of dorsal-stream areas have selectively enhanced activity during visuomotor tasks ([Culham, Gallivan, Cavina-Pratesi, & Quinlan, 2008](#); [Culham & Valyear, 2006](#)), but the same is not true for areas in the ventral stream (e.g. [Cavina-Pratesi, Goodale, & Culham, 2007](#)). Thus it might be that while the computational contribution of areas in the dorsal stream are more suited for visuomotor guidance, areas in the ventral stream provide information that can contribute to a greater variety of visual behaviour. However, specialization does not imply exclusivity. Ultimately visuomotor behaviour draws on information from both streams. It is this richness of information supply which provides the basis for an alternative explanation of visuomotor robustness after ventral-stream damage.

3. Integration as a basis of visuomotor robustness

I argued above, that ventral-stream areas are directly involved in the control of visuomotor behaviour. Such a viewpoint faces an obvious problem. How can we account for the apparently normal visuomotor behaviour of patients with ventral-stream lesions? The classical explanation for this visuomotor robustness involved the assumption that the ventral stream is only indirectly involved in the control of visuomotor behaviour. But as we have seen above, the assumption that we can objectively discriminate between a direct and indirect role of vision in action is not justified. We therefore need an alternative account of visuomotor robustness. Our alternative explanation is based on the following presupposition: Both the ventral and dorsal streams contribute useful visual information for visuomotor control, but in many conditions the information from the two streams contain some degree of redundancy. A typical example is provided by reaching for targets in depth. To estimate a target’s position in depth many different cues can be used ([Mamassian & Landy, 2001](#); [Landy, Maloney, Johnston, & Young, 1995](#)). Binocular disparity, vergence angle, motion parallax, vertical gaze angle, but also pictorial-depth cues such as familiar size and perspective cues can help us to establish the position of a target in depth. Some of those cues, such as the pictorial-depth cues, will come from ventral-stream areas, but others will not. It is plausible to assume that the brain will make use of many of those cues to achieve the best and most reliable estimate of a target position and thereby to produce an accurate reaching movement. However, not all of the cues are always needed to achieve a good estimate of the target-position. Thus, when some of those cues are no longer available either as consequence of brain damage or degradation of the sensory environment, the effects on reaching accuracy might be minimal. Consequently, no impairments will be observed. We know that in healthy subjects the effects of removing or distorting one depth cue are often hardly detectable (e.g. [Marotta et al., 1997](#); [Mon-Williams, Tresilian et al., 2001b](#); [Wann, Mon-Williams, McIntosh, Smyth, & Milner, 2001](#)). We should, therefore, not be surprised that the loss of one depth cue will leave a patient’s motor performance unaffected. In this context it is important to remind the reader that the demonstrations of visuomotor robustness after ventral-stream damage are based on single-case studies. Such single-case studies have substantially lower statistical power than group studies. This means that only substantial deficits lead to significant differences between normal and patient behaviour ([Crawford & Garthwaite, 2005, 2006](#)).

The explanation of visuomotor robustness based on the integration account differs in one respect from the classical or segregation account. The segregation-account assumes that the ventral stream is only indirectly involved in visuomotor control. The segregation account therefore implies that visuomotor control without an intact ventral stream can serve as a model of normal visuomotor control. This idea is rejected by the integration account. The integration account assumes that the visuomotor processes in such patients are different from the normal ones. In particular, it is assumed that ventral-stream damaged patients lost some of the relevant visual input. Consequently, their visuomotor processes will be more impoverished. This leads to two predictions: Firstly, normal visuomotor behaviour will be affected by cues, which are assumed to be processed in the ventral stream. Secondly, visuomotor behaviour of patients with ventral-stream damage is less flexible and more vulnerable in impoverished sensory environments.

Is there any evidence that cues processed in the ventral stream have an effect on visuomotor behaviour? Many pictorial illusions, such as the Ponzo, Ebbinghaus and Mueller-Lyer illusions, are based on pictorial-depth cues whose neuronal origin is assumed to lie in the ventral stream (e.g. Goodale & Milner, 2010). While initial reports claimed that visual illusions do not affect visuomotor behaviour (Aglioti, Desouza, & Goodale, 1995; Bridgeman, Lewis, Heit, & Nagle, 1979), this claim was frequently (but not always) contradicted by later studies (see Franz, 2001; Franz & Gegenfurtner, 2008). Moreover, two recent meta-analyses (looking at the effect of the Mueller-Lyer illusion on pointing and grasping) confirm that the effect of illusions on actions are significant, while often smaller than the effects on perceptual tasks (Bruno, Bernardis, & Gentilucci, 2008; Bruno & Franz, 2009). This finding is precisely what would be expected, if pictorial cues provide one out of many visuomotor cues. However, the interpretation of the effects of illusion on action has been dogged by controversy for many years (Smeets & Brenner, 2006). Moreover, a recent fMRI study (Murray, Boyaci, & Kersten, 2006) showed that pictorial illusions already have an effect on activation in primary visual cortex. This finding has cast doubt on the assumption that such illusions have a ventral-stream origin.

Less controversial is the neural origin of the familiar-size cue. This cue originates from the ventral stream. The familiar-size cue relies on our knowledge of the size of familiar objects. Obviously this information is only available for objects which can be recognized and object recognition involves the ventral stream (e.g. Karnath, Ruter, Mandler, & Himmelbach, 2009). If we recognize an object and know its physical size, we can use this information in a grasping task to adjust the opening of our hand to the size of the object. Furthermore, our visual system can also compare the size of the object's image on the retina to its known physical size and derive from this comparison an estimate of the object's distance to the observer. Consequently if we present an exemplar of an object, whose real size is smaller than its normal size, subjects will believe that the object has its well-known normal size and is just further away from the observer. If subjects use the familiar-size cue for grasping, we expect to see an exaggerated reaching amplitude and hand-opening. This is what McIntosh and Lashley (2008) found in their experiment – further evidence that ventral stream information is used in normal visuomotor control.

But what is the evidence for the claim that ventral-stream damage leads to reduced visuomotor flexibility? A number of studies on DF can be cited in support of this claim. Several authors showed that DF's reaching and prehension performance is impaired in the absence of binocular cues (Carey et al., 1998; Dijkerman et al., 1996; Marotta et al., 1997). Furthermore, Mon-Williams and colleagues showed in an elegant series of experiments, that DF relies almost exclusively on vergence and vertical gaze angle to guide her

hand to targets in depth (Mon-Williams, McIntosh et al., 2001a; Mon-Williams, Tresilian et al., 2001b; Wann et al., 2001). Healthy subjects can combine pictorial cues with binocular cues to estimate an object's distance in depth. DF cannot use pictorial cues and instead relies on binocular cues, motion parallax and extra-retinal information (such as vertical gaze angle) to estimate an object's distance in depth. Accordingly, when such information is removed her visuomotor performance falls well below the normal level.

In summary, there is evidence from both healthy subjects and DF that a ventral-stream deprived brain is not a good model of the normal visuomotor system. Instead patients without an intact ventral stream rely on a significantly smaller set of sensory cues to guide their actions than neurologically intact subjects. These findings support the integration account. It might therefore be useful to describe this account in more detail. The claim that multiple cues from areas across the visual cortex are involved in visuomotor behaviour should not be confused with the idea of a common representation. The common-representation hypothesis assumes that the visual cortex gives rise to one single, unified visual representation which forms the basis for all visual behaviour. As Milner and Goodale (1995) pointed out, such a view would be inconsistent with the normal visuomotor performance which was found across a range of tasks in DF. If all behaviour (including motor behaviour) were based on the same unified perceptual representation, perceptual deficits would be expected to lead to corresponding visuomotor deficits.

The alternative to a single visual representation is, however, not necessarily a strict segregation between vision for perception and action. Instead the alternative, suggested here, is the existence of multiple visual processes producing multiple visual cues, recruited from the entire visual cortex and combined in a flexible way to suit the requirements of the behavioural task. In this scenario there is neither a rigid divide between visual processes for action and perception nor the assumption that all visual processes will converge on one common representation. In the context of visuomotor control it may be more useful to think of those visual cues not as input but as constraints. The cues do not necessarily produce a new visual "representation" but constrain the selection process, which for a given visuomotor task leads to the optimal combinations of muscle activations. We can assume that the selection and combination of cues used for visuomotor behaviour will be guided by similar principles guiding the multisensory combination of cues for perceptual tasks (Ernst & Banks, 2002; Schrater & Kersten, 2000). One such principle of optimal cue-combination is that higher weights are given to more reliable cues. This has been confirmed by a number of studies (see Ernst & Buelthoff, 2004; Schrater & Kersten, 2000). It seems that this principle generalises to spatial reference frames. Byrne and Crawford (2010) recently demonstrated that the reliability and stability of sensory cues affects the relative contribution of egocentric versus allocentric information for memory-guided reaches.

Time might be another factor guiding the selection and combination of visual cues used in the control of motor behaviour (Greenwald, Knill, & Saunders, 2005). Actions often have to be executed within very tight temporal constraints, while at the same time some visual processes will take longer than others. It is therefore plausible to assume that the time constraints imposed by a motor task will affect the selection of sensory cues by which it is guided. For example, time constraints seem to play an important role in the selection of the neuronal pathways which are used to guide sensorimotor behaviour. Dramatic demonstrations of this are provided by the phenomenon of paradoxical movements (Glickstein & Stein, 1991). Paradoxical movements are near-normal movements observed under specific conditions in patients with movement disorders. A typical example is the striking contrast be-

tween catching and grasping, often observed in patients with Parkinson's disease (Majsak, Kaminski, Gentile, & Flanagan, 1998). While the seemingly easier task of grasping a stationary object is carried out slowly and with great difficulty, catching is carried out with ease and at normal speed. An experiment carried out in Parkinson patients with implanted deep-brain stimulators showed that paradoxical and non-paradoxical movements rely on different sensorimotor circuits (Schenk, Baur, Steude, & Boetzel, 2003). Furthermore, a study of a patient with post-traumatic ataxia allowed us to identify external temporal constraints as the most critical factor in triggering paradoxical movements (Schenk & Mai, 1999). Together, these findings suggest that the temporal requirements of the visuomotor task can determine the selection of sensorimotor circuits.

More specifically, De'Sperati and Baud-Bovy (2008) recently showed that the temporal characteristics of an action also determine what visual information is used to guide it. They found, that the flash-lag illusion affects only long-delay saccades. Interestingly, de Grave and Bruno (2010) also observed a link between saccade-latency and the effects of a visual illusion (the Mueller-Lyer illusion), but in their case long-latency saccades were less affected by the illusion. To make matters even more confusing, it has also been shown, that pictorial-depth cues become available at a shorter latency than binocular cues (van Mierlo, Louw, Smeets, & Brenner, 2009). These apparent contradictions may be due to differences in the employed tasks, motor responses and stimuli. Taken together this research suggests, that time is an important factor in determining what information is used in visuomotor control. However, it remains to be established how the temporal requirements of the task guide the selection of visual information in different conditions. But time is not the only factor. Findings from DF suggest that the memory-requirements of a visuomotor task also determine which visual brain structures are involved (for a discussion of this interesting topic, see: Franz, Hesse, & Kollath, 2009; Goodale, Jakobson, & Keillor, 1994a; Hesse & Franz, 2009; Rice-Cohen, Cross, Tunik, Grafton, & Culham, 2009; Rossit, Szymanek, Butler, & Harvey, 2010; Schenk & McIntosh, 2010).

To conclude, the integration account explains why patients such as DF seem to operate almost normally in a natural visual environment, rich in sensory cues, but show significant problems in a more impoverished sensory environment. It should be noted that a similar account was used to explain why the effect of illusions varies with the behavioural task (Geisler & Kersten, 2002; Hartung, Schrater, Buelthoff, Kersten, & Franz, 2005; Smeets, Brenner, de Grave, & Cuijpers, 2002). By accepting the integration account we also acknowledge that the ventral-stream deprived brain is not a neural model of the normal, visuomotor system. Moreover, as I will describe in the last section this account has implications for the future conduct of neuropsychological research.

4. Conclusions

Uncovering the contribution of ventral-stream areas to the control of visuomotor behaviour poses an interesting challenge. I argued above that ventral-stream areas are involved in the control of visuomotor behaviour, but unlike some of the areas in the dorsal stream they are not necessarily specialized for visuomotor control or perception. Instead they act as multipurpose visual tools. This means identifying their contribution to visuomotor behaviour using functional imaging is difficult. The functional-imaging approach typically relies on the activation-difference between vision-only versus vision-plus-action conditions (or the contrast between different types of actions) to identify action-relevant areas. In the case of multipurpose areas such differences cannot be expected. Multipurpose areas might contribute to both percep-

tual and motor tasks without necessarily being more active in either of them. The data from a recent functional imaging study, which contrasted the activity of areas AIP and LO in a vision-only task with two visuomotor tasks (i.e. reaching and grasping), demonstrates this problem (Cavina-Pratesi et al., 2007). They found that while AIP clearly emerges as a critical area for grasping, when contrasting *vision-only with grasping* or *grasping with reaching*, LO was not highlighted by either of these contrasts. However, far from being silent in all of those conditions, the examination of the bold-response in LO clearly demonstrated significant activity in all three conditions. Such a finding cannot demonstrate the potential relevance of LO for visually-guided action. But it illustrates the limitations of functional imaging in exploring the visuomotor role of those areas that are specialized in terms of their computational properties but not in terms of their behavioural role.

Neuropsychological examinations, therefore, becomes even more important. Examinations of patients with damage in the ventral stream can provide the evidence which functional imaging cannot. Regardless of whether those areas in the ventral stream are specialized for visuomotor control or not, if they are critically involved, damage to them should result in impaired visuomotor performance. However, when using this approach, it is important to take the sensory redundancy of visuomotor control into account. This redundancy implies that a given visuomotor task can be solved using a variety of different sensorimotor strategies and sensory cues. This insight prompts a change in research strategy. In the past, reports on DF and similar patients emphasized the patients' preserved visuomotor capacities. However, such preserved capacities do not provide unequivocal information about the ventral stream's role in visuomotor control. Visuomotor performance could be preserved because the ventral stream is not involved or because alternative sources of visual information are used to compensate for the missing ventral stream input. In contrast, visuomotor deficits after brain damage unequivocally demonstrate the critical role of the damaged area for the affected visuomotor task. It was DF's surprising visuomotor robustness which turned her into one of the most studied patients in the history of Neuropsychology. But it might be her more subtle visuomotor deficits which in future might provide the more lasting insights into the neural control of visuomotor behaviour.

Acknowledgment

I would like to thank my colleague Dr. Daniel Smith for turning my prose into readable English.

References

- Aglioti, S., Desouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, 5, 679–685.
- Alexander, G. E., Delong, M. R., & Crutcher, M. D. (1992). Do cortical and basal ganglionic motor areas use motor programs to control movement. *Behavioral and Brain Sciences*, 15, 656–665.
- Bridgeman, B., Lewis, S., Heit, G., & Nagle, M. (1979). Relation between cognitive and motor-oriented systems of visual position perception. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 692–700.
- Bruno, N., Bernardis, P., & Gentilucci, M. (2008). Visually guided pointing, the Muller-Lyer illusion, and the functional interpretation of the dorsal-ventral split: Conclusions from 33 independent studies. *Neuroscience and Biobehavioral Reviews*, 32, 423–437.
- Bruno, N., & Franz, V. H. (2009). When is grasping affected by the Muller-Lyer illusion? A quantitative review. *Neuropsychologia*, 47, 1421–1433.
- Byrne, P. A., & Crawford, J. D. (2010). Cue reliability and a landmark stability heuristic determine relative weighting between egocentric and allocentric visual information in memory-guided reach. *Journal of Neurophysiology*, 103, 3054–3069.
- Carey, D. P., Dijkerman, H. C., & Milner, A. D. (1998). Perception and action in depth. *Consciousness and Cognition*, 7, 438–453.
- Carey, D. P., Harvey, M., & Milner, A. D. (1996). Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. *Neuropsychologia*, 34, 329–337.

- Cavina-Pratesi, C., Goodale, M. A., & Culham, J. C. (2007). fMRI reveals a dissociation between grasping and perceiving the size of real 3D objects. *Plos One*, 2, 59.
- Crawford, J. R., & Garthwaite, P. H. (2005). Evaluation of criteria for classical dissociations in single-case studies by Monte Carlo simulation. *Neuropsychologia*, 19, 664–678.
- Crawford, J. R., & Garthwaite, P. H. (2006). Detecting dissociations in single-case studies: Type I errors, statistical power and the classical versus strong distinction. *Neuropsychologia*, 44, 2249–2258.
- Culham, J. C., Gallivan, J., Cavina-Pratesi, C., & Quinlan, D. J. (2008). fMRI Investigations of reaching and ego space in human superior parieto-occipital cortex. In R. L. Klatzky, B. MacWhinney, & B. Behrmann (Eds.), *Embodiment, ego-space, and action (Carnegie Mellon symposia on cognition series)* (pp. 247–266). New York, US: Psychology Press.
- Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, 16, 205–212.
- de Grave, D. D. J., & Bruno, N. (2010). The effect of the Muller-Lyer illusion on saccades is modulated by spatial predictability and saccadic latency. *Experimental Brain Research*, 203, 671–679.
- De'Sperati, C., & Baud-Bovy, G. (2008). Blind saccades: An asynchrony between seeing and looking. *Journal of Neuroscience*, 28, 4317–4321.
- Diedrichsen, J., Shadmehr, R., & Ivry, R. B. (2009). The coordination of movement: Optimal feedback control and beyond. *Trends in Cognitive Sciences*, 14, 31–39.
- Dijkerman, H. C., McIntosh, R. D., Schindler, I., Nijboer, T. C. W., & Milner, A. D. (2009). Choosing between alternative wrist postures: Action planning needs perception. *Neuropsychologia*, 47, 1476–1482.
- Dijkerman, H. C., Milner, A. D., & Carey, D. P. (1996). The perception and prehension of objects oriented in the depth plane. I. Effects of visual form agnosia. *Experimental Brain Research*, 112, 442–451.
- Dijkerman, H. C., Milner, A. D., & Carey, D. P. (1999). Motion parallax enables depth processing for action in a visual form agnostic when binocular vision is unavailable. *Neuropsychologia*, 37, 1505–1510.
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, 415, 429–433.
- Ernst, M. O., & Buelhoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, 8, 162–169.
- Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, 5, 457–459.
- Franz, V., & Gegenfurtner, K. (2008). Grasping visual illusions: Consistent data and no dissociation. *Cognitive Neuropsychology*, 25, 920–950.
- Franz, V. H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control. *Neuropsychologia*, 47, 1518–1531.
- Geisler, W. S., & Kersten, D. (2002). Illusions, perception and Bayes. *Nature Neuroscience*, 5, 508–510.
- Georgopoulos, A. P., & Ashe, J. (2000). One motor cortex, two different views. *Nature Neuroscience*, 3, 963.
- Georgopoulos, A. P., Kalaska, J. F., Caminiti, R., & Massey, J. T. (1982). On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *Journal of Neuroscience*, 2, 1527–1537.
- Glickstein, M., & Stein, J. (1991). Paradoxical movement in Parkinson's disease. *Trends in Neuroscience*, 14, 480–482.
- Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994a). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, 32, 1159–1178.
- Goodale, M. A., Jakobson, L. S., Milner, A. D., Perrett, D. I., Benson, P. J., & Hietanen, J. K. (1994b). The nature and limits of orientation and pattern processing supporting visuomotor control in a visual form agnostic. *Journal of Cognitive Neuroscience*, 6, 46–56.
- Goodale, M. A., Meenan, J. P., Buelhoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994c). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, 4, 604–610.
- Goodale, M. A., & Milner, A. D. (2010). Two visual streams: Interconnections do not imply duplication of function. *Cognitive Neuroscience*, 1, 64–66.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349, 154–156.
- Greenwald, H. S., Knill, D. C., & Saunders, J. A. (2005). Integrating visual cues for motor control: A matter of time. *Vision Research*, 45, 1975–1989.
- Hartung, B., Schrater, P. R., Buelhoff, H. H., Kersten, D., & Franz, V. H. (2005). Is prior knowledge of object geometry used in visually guided reaching? *Journal of Vision*, 5, 504–514.
- Hesse, C., & Franz, V. H. (2009). Memory mechanisms in grasping. *Neuropsychologia*, 47, 1532–1545.
- Hoff, B., & Arbib, M. A. (1993). Models of trajectory formation and temporal interaction of reach and grasp. *Journal of Motor Behavior*, 25, 175–192.
- James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain*, 126, 2463–2475.
- Karnath, H. O., Ruter, J., Mandler, A., & Himmelbach, M. (2009). The anatomy of object recognition-visual form agnosia caused by medial occipitotemporal stroke. *Journal of Neuroscience*, 9, 5854–5862.
- Mamassian, P., & Landy, M. S. (2001). Interaction of visual prior constraints. *Vision Research*, 41, 2653–2668.
- Landy, M. S., Maloney, L. T., Johnston, E. B., & Young, M. (1995). Measurement and modeling of depth cue combination – In defense of weak Fusion. *Vision Research*, 35, 389–412.
- Majsak, M. J., Kaminski, T., Gentile, A. M., & Flanagan, J. R. (1998). The reaching movements of patients with Parkinson's disease under self-determined maximal speed and visually cued conditions. *Brain*, 121, 755–766.
- Marotta, J. J., Behrmann, M., & Goodale, M. A. (1997). The removal of binocular cues disrupts the calibration of grasping in patients with visual form agnosia. *Experimental Brain Research*, 116, 113–121.
- McIntosh, R. D., & Lashley, G. (2008). Matching boxes: Familiar size influences action programming. *Neuropsychologia*, 46, 2441–2444.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). Oxford: Oxford University Press.
- Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46, 774–785.
- Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in 'visual form agnosia'. *Brain*, 114, 405–428.
- Mon-Williams, M., McIntosh, R. D., & Milner, A. D. (2001a). Vertical gaze angle as a distance cue for programming reaching: insights from visual form agnosia II (of III). *Experimental Brain Research*, 139, 137–142.
- Mon-Williams, M., Tresilian, J. R., McIntosh, R. D., & Milner, A. D. (2001b). Monocular and binocular distance cues: insights from visual form agnosia I (of III). *Experimental Brain Research*, 139, 127–136.
- Moran, D. W., & Schwartz, A. B. (2000). One motor cortex, two different views. *Nature Neuroscience*, 3, 963.
- Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience*, 9, 429–434.
- Plamondon, R., Stelmach, G. E., & Teasdale, N. (1990). Motor program coding representation from a handwriting generator model – The production of line responses. *Biological Cybernetics*, 63, 443–451.
- Rice-Cohen, N., Cross, E. S., Tunik, E., Grafton, S. T., & Culham, J. C. (2009). Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: A TMS approach. *Neuropsychologia*, 47, 1553–1562.
- Rossit, S., Szymanek, L., Butler, S. H., & Harvey, M. (2010). Memory-guided saccade processing in visual form agnosia (patient DF). *Experimental Brain Research*, 200, 109–116.
- Schenk, T., Baur, B., Steude, U., & Boetzel, K. (2003). Effects of deep brain stimulation on prehensile movements in PD patients are less pronounced when external timing cues are provided. *Neuropsychologia*, 41, 783–794.
- Schenk, T., & Mai, N. (1999). Time constraints improve reaching movements in an ataxic patient. *Experimental Brain Research*, 120, 214–218.
- Schenk, T., & McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, 1, 52–63.
- Schmidt, R. A. (1975). Schema theory of discrete motor skill learning. *Psychological Review*, 82, 225–260.
- Schrater, P. R., & Kersten, D. (2000). How optimal depth cue integration depends on the task. *International Journal of Computer Vision*, 40, 73–91.
- Scott, S. H. (2000a). One motor cortex, two different views – Reply. *Nature Neuroscience*, 3(10), 964–965.
- Scott, S. H. (2000b). Population vectors and motor cortex: Neural coding or epiphenomenon? *Nature Neuroscience*, 3, 307–308.
- Shaffer, L. H. (1992). Motor programming and control. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior II* (pp. 181–194). Amsterdam: North-Holland.
- Smeets, J. B. J., & Brenner, E. (1999). A new view on grasping. *Motor Control*, 3, 237–271.
- Smeets, J. B. J., & Brenner, E. (2006). 10 Years of Illusions. *Journal of Experimental Psychology: Human Perception and Performance*, 32, 1501–1504.
- Smeets, J. B. J., Brenner, E., de Grave, D. D. J., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research*, 147, 135–144.
- Stelmach, G. E., Mullins, P. A., & Teulings, H. L. (1984). Motor programming and temporal patterns in handwriting. *Annals of the New York Academy of Sciences*, 423, 144–157.
- Summers, J. J., & Anson, J. G. (2009). Current status of the motor program: Revisited. *Human Movement Science*, 28, 566–577.
- Todorov, E. (2000a). Direct cortical control of muscle activation in voluntary arm movements: A model. *Nature Neuroscience*, 3, 391–398.
- Todorov, E. (2000b). One motor cortex, two different views – Reply. *Nature Neuroscience*, 3, 963–964.
- Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, 7, 907–915.
- Ungerleider, L. G., & Haxby, J. V. (1994). 'What' and 'where' in the human brain. *Current Opinion in Neurobiology*, 4, 157–165.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. Mansfield (Eds.), *Analysis of visual behavior*. Cambridge, MA: MIT Press.
- van Mierlo, C. M., Louw, S., Smeets, J. B. J., & Brenner, E. (2009). Slant cues are processed with different latencies for the online control of movement. *Journal of Vision*, 9, 1–8.
- Wann, J. P., Mon-Williams, M., McIntosh, R. D., Smyth, M., & Milner, A. D. (2001). The role of size and binocular information in guiding reaching: Insights from virtual reality and visual form agnosia III (of III). *Experimental Brain Research*, 139, 143–150.
- Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, 3(Suppl.), 1212–1217.