



## Editorial

## Two visual streams for perception and action: Current trends

## 1. Introduction

This Special Issue of *Neuropsychologia* is a celebration and evaluation of the work of David Milner, who retired formally from his Chair at the University of Durham at the end of 2008. In the course of a distinguished career, David's work has informed many topics within cognitive neuroscience. However, his influence has thus far been felt most strongly via his collaboration with Mel Goodale on their *perception-action* model of primate vision (Goodale & Milner, 1992; Milner & Goodale, 1995; Milner & Goodale, 2006). The model proposes a functional interpretation for the two cortical visual streams, with the (occipito-temporal) ventral stream processing visual information for perceptual purposes, and the (occipito-parietal) dorsal stream providing visual guidance for movement. In the past two decades, the model has had a revolutionary effect within visual neuroscience, elevated the study of motor control to previously unthinkable prominence and inspired thousands of empirical studies. Moreover, its influence has reached beyond the boundaries of neuroscience, fuelling philosophical debates and even capturing the popular imagination (Goodale & Milner, 2004; Ramachandran & Blakeslee, 1998). The *perception-action* model thus provides an appropriate focus for this Special Issue.

To contribute to this Issue, we invited prominent researchers whose work is relevant to the broad scope of the model, many of them friends, former colleagues or students of David. Some have composed timely review articles; many have provided new empirical data. These contributions testify to the diversity of research and the depth of insight inspired by David's work, whilst showcasing the range of techniques available to modern cognitive neuroscience. The topics range from single-unit properties of parietal neurones to the behavioural organisation of reaching and grasping movements, from face perception to tool use and gesture production, from attentional orienting to the neural correlates of visual awareness. The techniques range from transient disruption of healthy brain function to clinical observations in chronic brain damage, from classical reaction time measures to kinematic analyses of movement, from primate neurophysiology to human functional neuroimaging. There are significant challenges to aspects of the *perception-action* model as well as evidence supporting its key claims. Our aim in this Editorial is to survey and summarize these contributions and to offer some context by relating them to one another and to the *perception-action* model.

## 2. Visual form agnosia

Many key insights leading to the development of the *perception-action* model have come from observations made with one woman, DF, who developed visual form agnosia following anoxic damage to her ventral stream, 21 years ago. Three contributions to this Issue continue her unique story, providing new data on DF's perceptual and visuomotor abilities. First, in an extension of prior reports (Carey, Dijkerman, Murphy, Goodale & Milner, 2006; Murphy, Carey & Goodale, 1988), Carey, Dijkerman and Milner (this issue) provide evidence that, whilst DF may apprehend allocentric spatial relationships between objects at a categorical level (e.g. left of, in-front of), she is severely limited in encoding their metrical aspects (how far to the left or in-front). The study also shows that DF's accurate aiming abilities go beyond simple unimanual movements to bimanual movements, thus extending her known visuomotor repertoire. By contrast, the experiment reported by Dijkerman, McIntosh, Schindler, Nijboer and Milner (this issue) implies strict limitations to this repertoire, since DF does not select her grip posture to minimize awkwardness during grasping, as do normal participants. This inapt grip selection is replicated in another individual with visual form agnosia and, in both cases, contrasted with a competent rotation of the grip to match the orientation of the object grasped. Dijkerman and colleagues interpret this pattern as reflecting impaired action planning with preserved action programming, where planning refers to the high-level selection of the type of action to be executed, and programming to its low level parameterization. Milner and Goodale (2008) have recently marked the planning-programming distinction as a critical boundary between ventral and dorsal stream influences on behaviour, so it will be interesting to see whether this distinction can be upheld, and more fully operationalised in the years to come.

The third contribution concerning patient DF makes a novel departure into the field of visual attention, with the striking observation that she has no trace of the typical advantage for within-object over between-object shifts, despite normal patterns of covert orienting in a standard Posner cueing task (De-Wit, Kentridge, & Milner, this issue). This speaks directly to an ongoing debate over the level of processing at which visual structure produces object-based effects in attention (e.g. Driver, Davis, Russell, Turatto, & Freeman, 2001). DF is an important test case because her early visual segmentation processes seem intact, as evidenced

for instance by her ability to individuate coloured tokens in Carey et al.'s study (this issue), or to direct actions at specific objects in Dijkerman et al.'s task (this issue). De-Wit et al.'s results thus imply that early visual segmentation processes are not sufficient to support object-based attention. Rather, the visual objects that normally shape the spread of attention may be form descriptions furnished by the lateral occipital complex (LOC), which are precisely lacking in DF.

### 3. Optic ataxia, and the dorsal stream control of action

Another neuropsychological condition of relevance to the *perception-action model* is optic ataxia, a disorder of visually guided reaching that follows dorsal stream damage. Interest in this disorder has burgeoned in recent years, yet optic ataxia presents many open questions, and several key puzzles to researchers. One such puzzle is that optic ataxic misreaching manifests typically only for extra-foveal targets, not for those that the patient can fixate. Jackson et al. (this issue) provide data to suggest that misreaching affects not only extra-foveal visual targets, but also proprioceptive targets that are displaced from the direction of gaze (see also Blangero et al., 2007). These data seriously question the status of optic ataxia as a specifically visuomotor disorder, and suggest the need for a broader functional explanation. Jackson et al. speculate that the core problem may be an inability to represent multiple locations *simultaneously*, and that this requirement arises whenever gaze is directed away from the reach target, regardless of the target modality. The obvious similarity between this proposal and attentional simultanagnosia, which often accompanies optic ataxia following bilateral parietal lesions, raises the important question of the functional relationship between attentional and visuomotor impairments following dorsal stream lesions. The same question has arisen recently elsewhere with the demonstration of attentional orienting impairments in the ataxic visual field of two patients with unilateral misreaching (Striemer et al., 2007), and this Special Issue sees the first attempt to address the question in one of these patients (Striemer, et al., this issue). Striemer and colleagues' tentative conclusion is that attention deficits and misreaching following superior parietal lobe lesions are functionally independent.

A further puzzling feature of optic ataxia is that extra-foveal misreaching can manifest in two distinct ways: as misreaching in the contralesional visual field or as misreaching with the contralesional hand (Perenin & Vighetto, 1988). So-called 'field' and 'hand' effects are present to different degrees in different patients, but their neuroanatomical bases have remained obscure. Blangero, Menz, McNamara and Binkofski (this issue) show fMRI evidence for an antero-posterior functional gradient within reach-related regions in and around the intraparietal sulcus, such that posterior regions are more active for reaching to the contralateral visual field, and anterior regions are more active for reaching with the contralateral hand. The strong prediction is that field and hand effects in optic ataxia should associate with damage to posterior and anterior parts of the reach-related network, respectively. We do not expect to wait long for a lesion study to test this prediction. Such studies offer vital clues to the functional and anatomical organisation of visually guided reaching, but a finer-grained understanding can only be achieved by considering functional imaging data and clinical observations alongside neurophysiological evidence from monkeys. Fearrain, Battaglia-Mayer, Genovesio, Archambault and Caminiti (this issue) do us a valuable service in synthesizing such diverse lines of evidence into a more comprehensive picture of the parietal lobe processes underlying the visual control of hand and eye, placing special emphasis on the depth dimension, so crucial for action in normal life. Finally, Himmelbach et al. (this issue) combine functional imaging and clinical approaches, mapping reach-related

activations in a patient with optic ataxia. Their findings have implications for understanding actions towards remembered visual targets, and will be discussed under the topic of delayed action. However, we turn first to the related, and even more debated, issue of visual illusions.

### 4. Illusions in action

The prediction that certain visual illusions should affect perceptual experience but not visually guided action has led to more publications, and more controversy, than any other aspect of the *perception-action model*. This prediction follows from the idea that many illusions of size, location or orientation operate via manipulation of visual context, whilst the action system represents intrinsic spatial properties of goal-objects within an egocentric frame of reference, independent of context. Early reports in favour of the prediction (e.g. Aglioti, DeSouza, & Goodale, 1995) met with both excitement and scepticism (see, e.g. Franz & Gegenfurtner, 2008, for a review), and subsequent studies examining the dissociation across a variety of illusions have produced mixed results. A constructive step was taken recently by Bruno, Bernardis, and Gentilucci (2008), who harnessed the variation in outcomes across studies for a meta-analysis of methodological factors influencing illusion strength in perception and action. Their first meta-analysis, which considered 33 studies of pointing towards the Müller-Lyer illusion, is now followed by a similar approach to 18 studies incorporating grasping responses to Müller-Lyer figures (Bruno & Franz, this issue). The analysis confirms reliable effects of the illusion on grip-scaling, and identifies the availability of visual feedback as the major factor moderating these effects. This conclusion receives direct experimental support from Franz, Hesse and Kollath (this issue), who find that the influence of Müller-Lyer figures on grasping is comparable to that on perception when a grasp is executed without visual feedback, but reduces progressively as visual feedback is made available for an increasing proportion of the movement. These converging results establish that grip programming is affected by Müller-Lyer figures, as is perception, but that these errors can be corrected online if the hand is seen approaching the target. Whilst this conclusion is at odds with the *perception-action model*, Franz et al. emphasise that it is so far limited to one illusion (Müller-Lyer) and one action response (grasping). This is pertinent, given that Bruno et al. (2008) first meta-analysis concluded in favour of a *relative* resistance of *pointing* movements to the Müller-Lyer figure, provided that vision was available at the time of action programming. The apparent differences between pointing and grasping may relate to different visual attributes of the Müller-Lyer figure being critical for their control (endpoint position vs. shaft length; Smeets, Brenner, de Grave, & Cuijpers, 2002).

### 5. Memory, perception and action

The *perception-action model* proposes that the dorsal stream is unable to store visual representations across temporal gaps, so that 'delayed' actions (directed towards remembered targets) must be guided by memory representations furnished by the ventral stream, thus falling prone to contextual illusions (see Westwood & Goodale, 2003, for a review). However, Franz et al.'s experiment (this issue) and Bruno & Franz's meta-analysis (this issue), strongly contest this idea. The apparent increase of illusory effects under delayed conditions may, in previous studies, have been driven by unavailability of visual feedback from movement in the delayed conditions. To further examine the differences between delayed and immediate actions, Hesse and Franz (this issue) present a comparison of grasping responses directed at non-illusory objects under closed- and open-loop visual guidance, and various levels of memory delay. The

results show that open loop actions are less accurate than closed-loop, and that further decrements in performance accrue with the addition of memory delays. The decrements associated with the delay effect, however, are well approximated by an exponential decay function, common across a wide range of memory-based tasks. Hesse and Franz suggest that differences between immediate and delayed actions are more parsimoniously explained by a single decaying memory trace than by a qualitative switch from dorsal to ventral stream guidance. Rogers, Smith and Schenk (this issue) use a very different approach to arrive at a similar conclusion. They reason that if immediate and delayed actions are mediated by separate pathways, there should be little transfer of prismatic adaptation between these two conditions. However, they find almost perfect transfer between immediate and delayed pointing, a finding which may be surprising given earlier prism-adaptation studies showing substantial reductions in transfer across even small changes in the visuomotor task (Baraduc & Wolpert, 2002; Scheidt & Ghez, 2007). The authors thus conclude that there may be considerable overlap between the visuomotor mechanisms supporting immediate and delayed action.

How can these conclusions be reconciled with Milner and colleagues' well-known observation that patients with optic ataxia following dorsal stream damage show improved action guidance under delayed conditions (Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Milner et al., 2001; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003)? Milner et al. (1999, 2001, 2003) argued that this 'paradoxical' improvement reflects a shift from the damaged dorsal system to the intact ventral system. However, the above-reviewed findings suggest that immediate and delayed action do not differ qualitatively in normal participants, thereby questioning the presumed switch. Himmelbach et al. (this issue) address this question by mapping the functional activation associated with immediate and delayed action in healthy people and in a bilateral optic ataxic patient (IG). These authors report robust activation of dorsal stream regions around IG's lesions during immediate reaching, in areas corresponding to activation foci for healthy participants. The most striking aspect of the data, however, is that an equivalent activation is reported for delayed reaching, suggesting that the same dorsal network is involved in reach execution regardless of whether the action is immediate or delayed. This pattern is consistent with the otherwise puzzling fact that optic ataxic misreaching is qualitatively similar, albeit less extreme, in delayed as in immediate conditions.

There are evidently problems emerging for the idea of a wholesale switch from dorsal to ventral stream control for delayed actions, but at least some of the findings reported in this Special Issue are more supportive of qualitative differences between immediate and delayed actions. First, Rice Cohen, Cross, Tunik, Grafton and Culham (this issue) applied transcranial magnetic stimulation over the LOC in the ventral stream or the anterior intraparietal (AIP) region of the dorsal stream during immediate and delayed grasp execution. They found effects of AIP stimulation for both grasping conditions, but only for delayed action in the case of LOC. This is consistent with the view that the dorsal stream participates in both forms of action, yet may also suggest a special role for the ventral stream in supplying visual information during delayed action. Second, Rossit et al. (this issue) set out to test the prediction that delayed but not immediate reaching should be compromised in patients with neglect, a disorder that Milner and Goodale (1995) have linked more closely with the ventral stream than the dorsal stream. In accord with the prediction, performance was impaired for pointing to remembered targets, with accurate reaching to physically present targets. Given some of the findings discussed above (Bruno & Franz, this issue; Franz et al., this issue), it may be important to establish what influence the availability of visual feedback during immediate action has upon this dissocia-

tion. Nonetheless, the result is an interesting one that adds weight to the idea that the immediate visual guidance of action is usually well preserved in neglect (e.g. Himmelbach & Karnath, 2003; McIntosh, Pritchard, Dijkerman, Milner, & Roberts, 2002; McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004).

Jax and Rosenbaum (this issue) and Dixon and Glover (this issue) also address the role of memory in action guidance. However, rather than focusing on visual memory supporting delayed actions, these studies look at implicit memory for the act itself, asking how recently-executed visually guided actions affect subsequent actions. Jax and Rosenbaum (2007) have previously reported such effects in an obstacle-avoidance task, showing that the spatial path of the hand on a given trial was biased towards the path taken on the preceding trial. In this Issue, they study the time-course of this phenomenon, showing that these sequential dependencies disappear when inter-trial intervals exceed 1 s. Dixon and Glover similarly report sequential dependencies between grasping movements, such that grip aperture is biased towards the aperture required in the preceding trial. These effects emerge despite inter-trial intervals well into the multi-second range (6–7 s), suggesting that not all such sequential dependencies are as ephemeral as Jax and Rosenbaum's. Although not explicitly envisaged within the *perception-action* model, these observations add detail to our knowledge of action guidance, and fit well within an emerging literature documenting hysteresis within the visuomotor system (Jax & Rosenbaum, 2007; Kent, Wilson, Plumb, Williams, & Mon-Williams, 2008; Whitwell, Lambert, & Goodale, 2008; Whitwell & Goodale, in press), which Jax and Rosenbaum (2007, this issue) refer to as 'visuomotor priming'.

Ball, Smith, Ellison and Schenk (this issue) studied priming effects of a more conventional sort, to test a surprising prediction that can be generated from the *perception-action* model. According to the model, only the ventral stream can support enduring representations of visual information (i.e., that can persist for 2 s or more), but this information will necessarily be coded in scene-based coordinates. Visuospatial memory should thus rely exclusively on allocentric representations, being unable to store egocentric representations. To test this prediction, Ball and colleagues measured spatial priming in a visual search task, comparing the efficacy of primes provided in allocentric, egocentric, or a combined frame of reference. They found robust spatial priming in all three conditions, with egocentric priming being, if anything, the most effective. This suggests that egocentric spatial representations can endure for at least 2 s. If the assumption that the dorsal stream is necessary for egocentric representation is correct, this result implies a capacity for enduring visual representations within dorsal stream structures.

## 6. Inter-stream interactions

Early research within the *perception-action* framework has focused, naturally enough, on functional dissociations between ventral and dorsal streams. More recently the complex issue of how these two streams interact has come to the fore. A nice example is provided by Kitadono and Humphreys (this issue) who report that the programming of target-directed actions enhances perceptual report at the targeted locations. This effect reduces pathological inattention to contralesional stimuli, thereby mirroring the perceptual facilitation obtained in normal participants at the target of impending reaches (Deubel, Schneider, & Paprotta, 1998). One mechanism by which such facilitation may arise is via spatially specific enhancement of early visual representations, which provide common input to dorsal and ventral streams (Schneider, 1995). Another interesting example of the interplay between dorsal and ventral processes in attention is proposed by Adamo and Ferber

(this issue), who found that pictures of objects within a rapid stream of images are more likely to survive the attentional blink if they have an action relationship with a tool shown earlier in the series. The authors propose that the visual short-term memory representation of the tool (e.g. a hammer) automatically evokes action affordances within the dorsal stream, in turn priming visual memory for action-appropriate objects (a nail). Crucially, the effect depends upon the physical properties of the tool, and is not driven by semantic associations, as it disappears when words rather than pictures are presented.

## 7. Parietal lobe function

Within the current literature, it is somewhat unclear how the *perception-action* model fits with theories of parietal lobe function more generally. Particular uncertainty exists over how the functions of the *inferior* parietal lobe (IPL) should best be characterized, and to what extent parietal specializations differ between the cerebral hemispheres. Milner and Goodale (1995, 2006) have proposed that the human IPL is a functional area, receiving inputs from both ventral and dorsal streams, which, in the right hemisphere at least, provides the basis for higher-level spatial representation. Ellison and Cowey (this issue), using dual-site transcranial magnetic stimulation, confirm a critical role for the right posterior IPL in an allocentric distance discrimination task, whilst also suggesting that optimal task performance is achieved in combination with analyses performed in the LOC region of the ventral stream. These data are clearly consistent with a characterisation of the right IPL as intimately concerned with spatial relationships. However, another contribution, from Singh-Curry and Husain (this issue), argues that insufficient consideration has been given to some attentional functions of the right IPL. They contend that this region is vitally important to the antagonistic roles of maintaining attention to current task goals, and orienting to salient new stimuli, and that these roles are not well represented by contemporary models of right parietal lobe function.

An interesting counterpart to the above is provided by Goldenberg (this issue), who authoritatively reviews and reassesses the clinical evidence for the association between apraxia and damage to the left parietal lobe. Goldenberg's thesis is that this link may hold only for the imitation of meaningless gestures and, in association with more widespread damage, the use of tools and objects. Goldenberg suggests that the left IPL is critical for the categorical apprehension of spatial relationships between objects or parts of objects, including the body. This novel proposal ascribes spatial functions to the left IPL somewhat complementary to those of the right IPL, and presents a significant challenge to the classically held belief in a left parietal locus for stored action patterns.

## 8. Beyond vision

The *perception-action* model is a model of the visual system, but Dijkerman and de Haan (2007) recently argued for a parallel distinction between perception and action within the somatosensory system. They suggest that this distinction corresponds to that between the body image and the body schema, with the body image providing information for body recognition and the body schema being used in guiding actions towards the self. Anema et al. (this issue) examined two stroke patients to explore the validity of this distinction. The patients were touched at various positions on their hand, and required to point directly to the touched position (body schema) or to the corresponding location on a drawing of a hand (body image). A classical double dissociation was found, with one patient failing on the body image task but not on the body schema task and the other patient showing the opposite pattern, provid-

ing further evidence that the body image and body schema are represented in separate neural networks.

A more direct link between the visual and tactile modality is examined by Brown, Morrissey and Goodale (this issue). The fact that there are bimodal neurons in the primate cortex, which respond both to tactile and visual input, and that these neurons can be recruited by visual stimulation alone if that stimulation occurs on or a near a body part (e.g. Graziano, Yap, & Gross, 1994), suggests that presenting visual information on the body surface might affect its discrimination. Brown and colleagues argue that since the number of tactile receptors, thus presumably also the number of bimodal neurons, is greater for the palm than for the back of the hand, visual information projected onto the palm may be represented more accurately. They tested this idea by comparing pointing accuracy towards visual targets projected onto the palm or the back of the participants' own hands, and contrasted this with pointing accuracy to equivalent locations on a fake hand. Accuracy was indeed higher for visual targets on the palm, but this was only found for the real but not the fake hand. This novel finding is satisfyingly complementary to that made by Kennett, Taylor-Clarke, and Haggard (2001), who showed that tactile acuity was improved when visuospatial resolution over the stimulated region of skin was enhanced with a magnifying glass. Together, these data suggest that the recruitment of bimodal neurons leads to behavioural gains. This is not only of theoretical interest but might also have some potential for rehabilitating sensory deficits in one or other modality. However, early attempts to exploit the clinical potential of this approach for patients with hemi-blindness (Schendel & Robertson, 2004) have not proved successful when tested in a larger cohort (Smith, Lane, & Schenk, 2008).

## 9. Face perception in the ventral stream

Discussion of the *perception-action* model often focuses on the visuomotor functions of the dorsal system. This may partly reflect the fact that the status of the ventral stream as critical to object and scene recognition was already well-established prior to the model's formulation. Recent functional neuroimaging work has further deepened our understanding of ventral stream involvement in visual perception. These studies have not only demonstrated that the ventral system processes the sensory signals that feed into our visual experience, but that activity within certain areas of the ventral stream is tightly correlated with the specific content of that experience. An elegant illustration of this was provided by Andrews, Schluppeck, Homfray, Matthews, and Blakemore (2002), who showed that activity in the fusiform face area (FFA) predicts whether the subject will report the face or the vase in Rubin's ambiguous figure. A further investigation of the role of the FFA in the perception of faces is provided by Davies-Thompson, Gouws and Andrews (this issue). They use the relatively new technique of fMR adaptation to test whether the FFA codes the identity of faces, independent of specific instance or viewpoint. If face-identity is coded within the FFA, then repeated presentations of the same face should produce fMR adaptation, even if different images are used. However, although adaptation was obtained for repeated presentations of the same image of a face, it was not found for different images of the same face, indicating that face-identity is not coded explicitly in the FFA.

## 10. Neural bases of visual awareness

Beyond the clearly vital roles that the ventral stream plays in visual perception, Milner and Goodale (1995, 2006) have more provocatively proposed an *exclusive* link between visual awareness and activity in the ventral system, implying that we may

never be directly aware of visual processing occurring within the dorsal stream. Unsurprisingly, philosophers, who have grappled with awareness for more than two millennia, have been greatly stimulated by this bold claim, and a rich dialogue between philosophers and neuroscientists has emerged. We are pleased that Clark (this issue) agreed to review the philosophical ramifications of the *perception-action* model, and delighted that he has done so in such an accessible way. Clark identifies several difficulties with the attempt to identify visual awareness exclusively with the ventral stream, from relatively direct empirical challenges (e.g. Schenk & Milner, 2006), to more theoretical concerns that the dorsal stream may contribute a 'feeling of presence' (Matthen, 2005), or ineffable 'directive content' to our awareness of the visual world (Nudds, 2007). Clark also provides a useful précis of Jacob and Jeannerod's (2003) critique of the perception-action view of consciousness. Jacob and Jeannerod suspect that Milner and Goodale do not compare like with like when they contrast the perceptual and action systems' relationship to consciousness, instead comparing relatively late stages of perceptual processing (which evoke awareness) with relatively early stages of the visuomotor processing (which do not).

Clark further discusses two broader issues that pose problems for any scientific attempt to pin down the mechanisms underlying conscious awareness. The first is that the commonly used criterion of reportability to infer the presence of awareness may turn out to be too narrow, causing us to overlook experiences which might have been reported but were not (e.g. Block, 2007). Even more fundamentally, our intuitive concept of conscious experience as a unitary entity may need to be replaced by a looser concept of consciousness as a complex combination of many streams and layers of experiences, so that simple questions regarding the presence or absence of consciousness may be the wrong ones to ask (e.g. Dennett, 1991). Despite, or perhaps partly because of such concerns, Clark concludes that the *perception-action* model has made a valuable and considerable contribution to the philosophical debate about consciousness.

## 11. Conclusion

A similar verdict holds, yet more emphatically, for the impact and value of the model within visual neuroscience, where it has advanced knowledge, and stimulated innovative research, and sometimes fierce debate, for nearly two decades. The eagerness of so many esteemed colleagues to contribute to this Special Issue in honour of David Milner, and the quality and diversity of their submissions, is ample evidence for this conclusion.

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