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Do we have distinct systems for immediate and delayed actions? A selective review on the role of visual memory in action

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ABSTRACT

The perception-action model with its assumptions of distinct visual pathways for perception and visuomotor control has been highly influential but also contentious. The controversy largely focused on the evidence from studies on perceptual illusions and this scientific field has been reviewed quite a few times in recent years. In contrast another aspect of the model, namely the role of visual memory in action control, received comparatively little attention. With respect to visual memory the perception-action model proposes that only the perceptual or ventral stream can maintain a sustained representation of the visual world while the visuomotor system or dorsal stream has to rely on currently available visual information. Consequently, visual information from the dorsal system cannot guide actions that are based on memorized visual information. We call this feature of the perception-action model: the dorsal amnesia hypothesis. There are at least two reasons for why this hypothesis is of special relevance. Firstly, it provides a particularly clear criterion to distinguish between functions of the ventral and dorsal stream. Secondly, this hypothesis led to some unexpected discoveries which provided particularly compelling evidence in favour of the model. In this review, we will revisit all relevant empirical areas, ranging from physiological examinations and neuropsychological studies to behavioural experiments in neurologically intact participants. Based on this review, we conclude that the dorsal amnesia hypothesis is in our view no longer tenable.

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In 1992, Goodale and Milner suggested that the primate visual system consists of two distinct visual systems (Goodale & Milner, 1992). According to this view, the cortical visual system originates in the primary visual cortex, V1, and then splits into a dorsal stream which projects into the posterior parietal cortex and a ventral stream projecting into the regions of the temporal cortex. Onto this anatomical division they mapped a functional division: the ventral stream is assumed to support visual perception and the dorsal stream is associated with functions relating to the visual guidance of actions. This

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model, here called the 'the perception-action model', provided a good account for a surprising set of neuropsychological observations in patient DF. Following carbon-monoxide poisoning, DF was unable to reliably discriminate objects on the basis of their form, size or orientation. Despite these profound perceptual deficits, she reliable adjusted her hand during reaching and grasping movements to the form, size and orientation of target objects (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). Within the framework of the perception-action model this counterintuitive dissociation between preserved visuomotor control and impaired perception could be explained. It seemed that in DF's case the ventral or perceptual system had been profoundly impaired while the dorsal or visuomotor system had been left largely intact. This neuroanatomical interpretation received support from early structural scans of DF's brain (Milner et al., 1991) and with some reservations also from a later structural and functional MRI study (Bridge et al., 2013; James, Culham, Humphrey, Milner, & Goodale, 2003).[1] The behavioural dissociation between perception and action not only suggested the existence of two anatomically distinct and functionally specialized visual systems but also pointed to the surprising independence with which these two systems could operate (Milner & Goodale, 1995, 2006).

Prior to the formulation of the perception-action model, other researchers had already suggested that the visual system might consist of two distinct subsystems (Schneider, 1969; Trevarthen, 1968; Ungerleider & Mishkin, 1982). In fact, it was Ungerleider and Mishkin (1982) who introduced the distinction between ventral and dorsal visual streams and thereby provided a first anatomical characterization of the two systems to which Milner and Goodale referred to in their model. However, while the functional characterization of the two-visual pathways suggested by Ungerleider and Mishkin appeared to be somewhat arbitrary, the functional division suggested by Milner and Goodale seemed highly plausible in the context of an evolutionary approach to the understanding of the primate visual system. More importantly, the distinction between visual systems for perception and action proved to be conceptually fertile because it seems obvious that those two functions require very different forms of visual processing. A perceptual system whose main purpose is to recognize objects and scenes and to understand the relation of objects within a scene obviously needs to have the capability to identify those aspects of the visual world irrespective of the conditions under which these objects and scenes are seen. Thus, it is important that the perceptual system extracts

invariances that are not affected by the position of the observer, the illumination of the scene, or any other conditions that are incidental to the current observational situation and irrelevant for object identification. This seems in contrast to the requirements of the action-system. In order to plan and execute an action, the position of the observer (and now actor) to the object is a critical parameter that needs to be taken into account for a successful interaction with the object. This distinction between a perceptual system concentrating on invariant features of objects and scenes and an action system taking account of observer-relative features allowed Goodale and his colleagues to derive predictions that could also be tested in healthy observers.

This meant that the explanatory power of the model is not restricted to one domain of psychology (e.g., neuropsychology) but touches upon other domains as well (e.g., anatomy and physiology of the visual system and psychophysics). This explains why the model proved to be very influential. Accordingly, the model and its implications have been reviewed many times in the past. For example, numerous reviews examined the claim that visual illusions affect perceptual performance more than visuomotor performance (Bruno, 2001; Carey, 2001; Franz & Gegenfurtner, 2008; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016) and several recent reviews also examined the neuropsychological evidence for the model (e.g., Milner & Goodale, 2008; Schenk & McIntosh, 2010; Schenk, 2010; Westwood & Goodale, 2011). But one aspect of the model, namely its claim that the dorsal stream has only a very short visual memory, received comparatively little attention and is still seen as largely uncontroversial (see Heath, Neely, Krigolson, & Binsted, 2010). Hence, this topic will be the focus of this review paper.

Milner and Goodale (1995, 2006) argued that the dorsal visuomotor system cannot store relevant visual information for more than one or at most 2 sec.[2] As we move around, we change our position and thus perspective on objects all the time. However, for successful interactions with the world, only the current perspective and the current spatial relationship between observer and goal object are relevant. Hence, it is expected that the dorsal system will only act on current information and has neither the need nor the capability for storing visual information over longer periods of time (see Milner & Goodale, 2006, pp. 41, 174, 246ff). Consequently, whenever an action has to be based on previous (remembered) information that is stored in visual memory, the visual input for this action has to come from the ventral perceptual stream (Milner & Goodale, 2006, pp. 137, 172, 246, 248). This assumption leads to a number of interesting predictions. For example, it is expected that perceptual illusions which presumably originate in the ventral stream will affect visual actions

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[1] In the case of DF, brain damage resulted from carbon monoxide poisoning leading to diffuse and widespread lesions. A recent MRI study provided a detailed characterisation of the pathological changes in DF's brain (Bridge et al., 2013). Bridge et al. (2013) compared the thickness of DF's cortex with that of healthy, age-matched controls. As expected, thickness of LOC differed substantially between patient DF and the control participants, but the same was also true for the posterior portion of the intraparietal sulcus (IPS). In fact all examined visual cortical areas with the exception of area V1 and MT were significantly thinner in DF than in healthy controls. This finding prompts the question of how appropriate it is to describe DF as a patient with selective damage to the ventral streams.

[2] In fact, Westwood and Goodale (2003) argued that this period is even shorter. According to their real-time view of action, the dorsal system relies on 'just-in-time' computations. The necessary retinal information will have to be present at the time the movement is programmed. This does not happen until the decision to act has been reached (see Milner & Goodale, 2006, p. 247). Consequently, whenever the relevant visual information is withdrawn prior to the participants receiving their go-signal, the ventral stream needs to provide the relevant visual information to guide the forthcoming visuomotor act.

performed after a delay (and thus relying on visual memory) even though the very same illusions will have little impact on actions performed without delay (and thus relying on real-time visual information). It can also be expected that a patient with selective lesions in the ventral stream, like patient DF, will fail in visuomotor tasks that introduce a delay between the presentation of the visual target information and the initiation of the visuomotor response even if she demonstrated normal performance in the real-time versions of those tasks. Both predictions seemed to be confirmed in previous studies (Goodale, Jakobson, & Keillor, 1994a; Westwood & Goodale, 2003). However, the most impressive confirmation for this prediction of the perception-action model came, without doubt, from patients suffering from optic ataxia. These patients have lesions in cortical areas that are associated with the dorsal stream. They misreach when performing reaching movements to visual targets, and their issues are particularly pronounced when they are prevented from directly looking at the target while performing their actions (Borchers, Muller, Synofzik, & Himmelbach, 2013; Perenin & Vighetto, 1988). According to the perception-action model, these patients exemplify the behaviour that can be expected when the dorsal stream is damaged; namely they have problems processing visual information for the guidance of actions (Goodale, Meenan, et al., 1994b; Milner & Goodale, 1995, 2006). It is interesting to consider what happens if such patients are asked to perform their movements on the basis of visual information held in their memory. Given the dorsal stream's inability to store visual information, neither healthy actors nor patients can base their actions on visual information mediated by the dorsal stream. Instead they have to rely on visual information from the only visual system capable of storing visual information — the ventral stream. In the case of healthy participants, it can be expected that visuomotor behaviour will become less accurate and more variable when a delay is introduced. The reason for this prediction is that visual information after a delay will have to come from the ventral stream and is therefore not optimized for visuomotor control. Again, this prediction was tested and confirmed (Westwood, Heath, & Roy, 2001). Yet, more interestingly, the exact opposite would be predicted for patients suffering from optic ataxia. Patients with optic ataxia will, after delay, also draw the sensory input for their visuomotor behaviour from the ventral stream and even though this ventral information is not optimal for visuomotor control, it is still much better than the lesion-compromised visual information held in the dorsal stream of those patients. Consequently, optic ataxia patients are expected to show more accurate reaching performance when the visual target is held in memory as compared to situations in which the target remains visible. This is a truly surprising, some might even say paradoxical, prediction that could, however, be confirmed in subsequent experiments (e.g., Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999).

In this review article, we will re-examine the hypothesis that the dorsal stream does not possess a memory for visual information. For the sake of brevity, we will call this hypothesis "*the dorsal amnesia hypothesis*". The claim of dorsal amnesia is important for two reasons. Firstly, it provides a very clear criterion to distinguish between tasks that involve the ventral stream and those that do not. Whenever, the relevant visual information for action has to be kept in memory for at least 2 s (or according to the real-time view even for just a few milliseconds; see Westwood and Goodale (2003)), the ventral stream becomes critically involved in the visual guidance of the corresponding visuomotor act. This allows us to derive many precise predictions and thus allows good tests for the validity of the perception-action model. Moreover, the precision of this criterion sets it apart from other properties that have been used to describe the functional properties of the ventral and dorsal stream within the perception-action model. As has been noted elsewhere, most of the other distinguishing properties suggested to indicate dorsal versus ventral stream processing (e.g., explicit versus implicit processing; indirect versus direct visuo-motor relationships, planning versus programming) are more controversial and often poorly operationalised (Clark, 2009; Jeannerod & Jacob, 2005; Milner & Goodale, 2006; Schenk, 2006, 2010). The second reason why the dorsal amnesia claim is of special relevance for the status of the perception-action model relates to the novelty of one of the findings predicted by this hypothesis. As described above, this hypothesis correctly predicted that patients with optic ataxia are less impaired when forced to base their actions on memorized visual targets as compared to visible targets. For other findings put forward in support of the perception-action model, like the observations that both visual illusions as well as ventral-stream damage affect visual perception more strongly than action, alternative accounts without a dual-system assumption have been offered (Dassonville, Bridgeman, Bala, Thiem, & Sampanes, 2004; Franz & Gegenfurtner, 2008; Schenk, 2010, 2012a, 2012b on ventral stream damage). However, in the case of the memory-induced paradoxical improvement of optic ataxia patients, it seems hard to conceive of an account that does not assume two separate visual systems with different properties and different functional roles. Clearly this finding gives special weight to the dorsal amnesia hypothesis. It is therefore of interest to closely scrutinise the empirical basis of this hypothesis.

The most recent comprehensive review on this topic came to the conclusion that the dorsal amnesia hypothesis is overwhelmingly supported by empirical studies (Heath et al., 2010). However, the validity of a theory is not decided by the quantitative relationship between the studies in its favour and those in opposition. Instead its validity must be decided by its ability or inability to account for challenging evidence and its potential to predict novel and unexpected effects. Accordingly, we will focus in our review on findings that are either particularly difficult to explain without recourse to the dorsal amnesia hypothesis, or contradict key features of this hypothesis. By its very nature such a review will be selective.

Our review paper is divided into seven sections. The first section will describe evidence from physiological, fMRI and TMS studies to examine the claim that ventral and dorsal regions differ in their ability to maintain visual representations and in their contribution to immediate versus memory-based

visuomotor acts. The second section will review the claim that ventral-stream damage impairs memory-based visuomotor behaviour. The third section looks at the complementary prediction for patients with dorsal-stream damage who were found to produce better visuomotor behaviour when guided by information from visual memory. The next three sections will look at evidence for the dorsal amnesia hypothesis from healthy humans. The fourth section reviews studies examining the impact of memory intervals on motor performance. The fifth section assesses the prediction that visual illusions affect visuomotor behaviour more strongly when the motor response is based on memorized visual information. The assumption about illusions and their effect on different types of action is to some extent a special case of the more general assumption that allocentric or scene-based spatial information contributes more to memory-based as compared to immediate visuomotor behaviour. This assumption will be examined in our penultimate section. Finally, in our seventh and final section, the arguments will be summarized and the implications for the perception-action model discussed.

1. A visual path with no memory? Evidence from neurophysiology, fMRI and TMS

The dorsal amnesia hypothesis assumes that visual representations in the dorsal stream are too transient to support memory-based actions. Both electrophysiological recordings from dorsal-stream neurons in non-human primates and fMRI studies on cortical areas situated in the dorsal stream can be consulted to address this question. The few non-human primate studies that have looked directly at the time-course of spiking activity in parietal regions associated with visually guided hand movements (e.g., AIP, area 7a) or visually guided saccades (LIP or area 7a) found evidence of sustained activity for several seconds that remained at a high level during the retention interval in visual short-term memory tasks (Gnadt & Andersen, 1988; Murata, Gallese, Kaseda, & Sakata, 1996; Snyder, Batista, & Andersen, 1997). We are not aware of a study that compares the time course of single-unit activity directly between dorsal and ventral stream areas, and to our knowledge no statistical test comparing the prevalence of sustained versus non-sustained spiking visual neurons in dorsal versus ventral stream areas has been reported. Thus, we turn to fMRI studies where recently a number of studies examined the capacity for sustained activity in human dorsal stream areas. An early attempt to locate areas of the human visuomotor pathway using fMRI employed a behavioural task that required participants to memorize the visual target for their pointing responses for as long as 9 sec (Connolly, Andersen, & Goodale, 2003). Given that despite this delay robust dorsal-stream activity could be found, the conclusion seems to be that the dorsal stream can retain the relevant information for several seconds. A few recent studies confirmed this conclusion more directly. In a series of experiments, Christophel and colleagues (Christophel, Cichy, Hebart, & Haynes, 2015; Christophel, Hebart, & Haynes, 2012)

used the technique of multi-voxel pattern analysis to determine whether regions of the posterior parietal cortex can retain information about a visual stimulus after its removal. They found that the activity in these regions is sufficiently precise and sustained to allow the accurate classification of the presented stimulus even several seconds after its removal. Christophel et al. (2012) concluded that regions within the posterior parietal cortex, some of which have been associated with reaching and grasping behaviour, contribute to visual short-term memory. Himmelbach et al. (2009) and Fiehler, Bannert, et al. (2011) went one step further and examined whether there was any fMRI evidence to support the claim that when a delay is introduced control for the visual guidance of action shifts from dorsal to ventral stream regions. Fiehler, Bannert, et al. (2011) compared brain activity for delayed and non-delayed visuomotor tasks in a group of healthy participants and Himmelbach et al. (2009) examined the same contrast and also included a patient with optic ataxia. Both studies found robust dorsal-stream activity for both immediate and delayed tasks. This was true for healthy observers and also for the patient suffering from optic ataxia (Himmelbach et al., 2009). Thus, neither single-unit recordings on monkeys nor evidence from fMRI studies on humans provide support for the presumed transient nature of dorsal stream activity or for the claim that tasks requiring actions to remembered visual targets induce a switch from dorsal to ventral-stream control of action.

However, such findings cannot preclude a modified version of the dorsal amnesia hypothesis. This modified version suggests that while the dorsal-stream on its own cannot maintain visual representations, it can support memory-guided action with additional input from ventral stream areas. This model can reconcile the neuropsychological findings from DF (ventral stream damage) with the fMRI results obtained in healthy participants. DF's apparent failure to perform normally in memory-guided action conditions is explained by the fact that the ventral input to the dorsal stream, which becomes crucial during a memory-guided action, is missing or at least severely compromised. The finding of sustained fMRI activity in dorsal stream areas in neurologically intact humans is explained by assuming that this activity depends on input from the ventral stream. In fact, support for this modified hypothesis has been reported by Singhal, Monaco, Kaufman, and Culham (2013). Specifically, Singhal et al. (2013) found re-emerging activity in the ventral stream (area LO) around the time the delayed motor response was initiated. They suggested that the re-activation of ventral area LO constitutes support for the claim that during delayed action, visual input from the ventral stream becomes critical for successful visuomotor performance. There are, however, two reasons why one might be hesitant to accept this interpretation. Firstly, claims of a temporal correlation between behaviour and BOLD activity have to be treated with caution given the multi-second lag that characterizes the relationship between neuronal activity and its correlated BOLD signal. Secondly, and more importantly, Singhal et al.'s (2013) interpretation of their data presumes a false dichotomy. They

contrast two possibilities: (1) both immediate and delayed actions are served exclusively by the dorsal stream or (2) immediate actions are served by the dorsal stream and delayed actions are served by both the dorsal and the ventral stream. The fact that ventral-stream activation is found in the delayed action condition is taken as evidence that option (2) is correct. However, this reasoning does not take into consideration the existence of another plausible third possibility: Immediate and delayed actions are *both* served by information from dorsal and ventral sources. This third possibility is not ruled out by the fMRI findings showing ventral activation during delayed action and it is in fact the one which we find most plausible and which also received some support from recent fMRI studies showing that area LO is indeed involved in the immediate processing of grasp relevant object properties such as object weight and size (Gallivan, Cant, Goodale, & Flanagan, 2014; Monaco et al., 2014). Thus, conclusive evidence against option (3) and for option (2) would require finding ventral activity for delayed actions only but not for immediate actions, but this yet has to be demonstrated.

Given the relatively poor temporal resolution of the fMRI method, transcranial magnetic stimulation (TMS) might provide a better option to test the idea that the ventral stream is crucially involved in visuomotor behaviour based on memorized visual information. TMS allows us to temporarily interfere with the function of a given brain area and to study the effect of such interference on a given type of behaviour. In case of the (modified or unmodified) dorsal amnesia hypothesis, we would expect that interference in area LO, the visual form area in the ventral stream, should disrupt specifically memory-based visuomotor behaviour. Rice-Cohen, Cross, Tunik, Grafton, and Culham (2009) tested this prediction using double-pulse TMS over LO (ventral stream) and AIP (dorsal stream). They reported that TMS over AIP affected both immediate and delayed grasping while only delayed grasping was affected by TMS over LO. At first glance, these findings seem to support the modified dorsal amnesia hypothesis, i.e., the dorsal stream is involved in both types of action, whereas the ventral stream contributes only to memory-based action. A more careful look at the findings casts however doubt on this interpretation. In the context of the perception-action model, the grasping response is typically considered the visuomotor equivalent of a size-discrimination judgement and the maximum opening of the hand during the grasp or the Maximum Grip Aperture (MGA) is seen as the visuomotor equivalent of a size-judgement (see for example, Aglioti, DeSouza, & Goodale, 1995; Ganel, Chajut, & Algom, 2008; Goodale et al., 1991). Following this logic, we would expect that MGAs (or more precisely the relationship between MGAs and object size) are used to judge whether a given area is involved in the visual guidance of grasping or not. However, the only variables which were significantly affected by TMS in the study by Rice-Cohen et al. (2009) were peak grasping velocity (i.e., the speed with which the hand was opening during the grasp) and the normalized time at which this peak occurred. Peak grasping velocity was increased when TMS was applied over LO during the delayed-grasping condition, and this peak occurred earlier when TMS was applied over

AIP. It remains to be explained why disruption of the very area that presumably provides the relevant visual target information for the grasping response should have no significant effect on MGAs but result in a speeding up of the hand-opening response and shift the velocity peak of that response to an earlier time point. To sum up, the findings from the study by Rice-Cohen et al. (2009) are certainly intriguing but their meaning is not yet clear.

TMS is, however, not the only approach that can be used to study the contribution of the ventral stream to memory-based action. If temporary disruption of the ventral stream is expected to interfere with memory-based action, permanent damage to the ventral stream should certainly cause a profound difficulty in this domain. We will turn to this prediction in the next section.

2. Trapped in the present. How ventral-stream damage affects memory-based action

The conclusion that ventral stream damage impairs the ability to perform memory-based visuomotor acts received initial support from a classic study conducted by Goodale, Jakobson, et al. (1994a). In this study, DF was first asked to grasp target objects placed in front of her. Her ability to adjust her hand-opening to the objects' size seemed normal. Next, she was again asked to grasp objects but this time vision of the target object was removed as well as the object itself. After a delay of 2 s, she was prompted to perform a grasping movement directed at the initially presented target object which was no longer on the table. It turned out that in this condition her performance was significantly worse than that of healthy control participants (Goodale, Jakobson, et al., 1994a).

More evidence for DF's failure to produce accurate memory-based visuomotor responses was reported for pointing to visual targets as well as for making eye-movements to visual targets (Milner, Dijkerman, & Carey, 1999; Rossit, Szymanek, Butler, & Harvey, 2010). However, at least in the case of the delayed grasping study, there is an obvious confound that might just as well account for DF's poor performance. While DF was waiting for the tone signalling the start of her grasping movement, the target object was physically removed from the table. Thus, DF had to pretend (or pantomime) a grasping movement and had to return to the start position without having had the chance to touch the real object and thus to compare her initial guess with the haptic information received when touching the real object. In short, Goodale et al.'s (1994a) grasping study compared a condition of real grasping and real haptic feedback with a condition using a delay and requiring a pantomime grasp that prevented haptic feedback. So the question arises, if it is possible that the lack of haptic feedback rather than the need to consult memorized visual information may account for DF's poor performance. Schenk (2012a, 2012b) addressed this question. DF had to perform a grasping task with the target object presented in a mirror setup. The target object was visible but perceived at its mirror position. At the mirror position a real object was placed in some conditions, but not in others. This setup ensured that

the visual target information was always available, even in conditions where no real object was present. As a consequence, it was possible to dissociate the availability of visual target information from the availability of haptic target information. As expected, DF produced normal reach-to-grasp movements when both visual and haptic information were available. However, her performance dropped to chance level when the haptic information was withdrawn (Schenk, 2012a, 2012b).[3] These findings suggest that it may have been the lack of haptic feedback rather than the

introduction of the delay that caused DF's poor performance in Goodale et al.'s (1994a) delayed grasping task.[4] More importantly these findings show the need for a study that examines the impact of temporal delays and haptic feedback on DF's visuomotor behaviour independently from each other. A few years ago, we used a posting paradigm to address this issue (Hesse & Schenk, 2014). In this paradigm, participants were asked to post a hand-held card into a slot whose orientation varied from trial to trial. This task was contrasted with an orientation-matching task, where participants rotated the hand-held card to match its orientation with that of the slot (see also Hesse, Franz, & Schenk, 2011 for a discussion of this paradigm). This is the same paradigm Milner et al. (1991) used to demonstrate DF's failure in orientation-matching (i.e., the perceptual task) but her near-normal behaviour in posting (i.e., the visuomotor task). We employed the same contrast but added a few additional conditions in which we manipulated the availability of visual feedback and the duration of the delay between the disappearance of the target information and the initiation of the posting movement. Surprisingly, all these careful manipulations of delay and visual feedback proved to be irrelevant. DF performed without error in all tested immediate and delayed posting conditions. Only in the orientation-matching condition her performance fell outside the normal range. This finding shows that, contrary to the predictions of the dorsal amnesia hypothesis, not all memory-based visuomotor behaviour is impaired by ventral stream damage. This means the claim that any normal memory-based visuomotor action is impossible with a damaged ventral stream is refuted and thus one of the main pieces of evidence for both the original and the revised dorsal amnesia hypothesis has been eliminated.

Some readers might feel that this conclusion is somewhat immoderate. Evidence for problems in delayed actions has been provided in three different behavioural paradigms: grasping, pointing and voluntary, saccadic eye-movements. This evidence it seems cannot be negated by just one failure to obtain the same result in a single type of visuomotor behaviour, i.e., posting. However, in our opinion the evidentiary status of supporting and challenging studies is not equivalent in this context. Supporting studies are less conclusive than dissenting studies for several reasons. The first reason relates to a simple point of logic. A hypothesis that makes a universal claim, e.g., all actions based on visual memory are impaired when the ventral system is impaired,

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[3] One reviewer asked us to comment on a study by Whitwell, Milner, Cavina-Pratesi, Byrne, and Goodale (2014) that challenged Schenk's (2012a, 2012b) interpretation of the influence of haptic feedback on DF's grasping performance. They contrasted two interpretations: the calibration hypothesis (Schenk, 2012a, 2012b) and the touch hypothesis (Milner, Ganel, & Goodale, 2012). The calibration hypothesis claims that DF uses haptic feedback to calibrate the visual information used for grasping; the touch-hypothesis assumes that it is the mere contact with a real object that will lead to the involvement of the dorsal stream and improves DF's grasping performance. In other words, the calibration hypothesis assumes that the haptic information must be informative about object size whereas the touch hypothesis predicts that non-informative haptic feedback will also improve DF's performance. Whitwell et al. (2014) employed a mirror-setup to decouple the visual and haptic properties of target objects. In one condition, the visual size of the target object varied but its haptic size remained constant. DF's grasping performance in this condition remained within the normal range. Whitwell et al. (2014) took this as evidence for the touch-hypothesis. We would like to make two comments. First this debate is not really relevant to the issue at hand. The fact that DF's performance is impaired when no real object is present remains undisputed. Accordingly, the fact that Goodale, Jakobson, et al. (1994a) confounded the introduction of a delay with the removal of the target object in their neuropsychological studies on delayed grasping remains problematic regardless of how we explain the detrimental effect of removing the physical object. Secondly, the findings by Whitwell et al. (2014) do not provide compelling support for the touch hypothesis since both touch and calibration hypothesis predict normal grasping performance in the constant-haptic size condition albeit for different reasons. The touch hypothesis assumes that informative haptic feedback is irrelevant for accurate grip scaling. The calibration hypothesis predicts that the experience of a constant haptic size in the face of varying visual size will convince participants of the irrelevance of the visual information. Hence, they will give less weight to the available visual information which will in turn weaken the relationship between visual size and grasp performance (as measured by the slope of that linear function). This is expected to happen for DF and controls alike and thus DF's performance will remain within the normal range. A further problem of Whitwell et al.'s study (2014) relates to DF's performance in the corresponding visual-size estimation task. When considering the absolute value of the slope linking real visual size and DF's estimated size, her performance in the perceptual task is better than in any of the grasping tasks. This poses a problem for the entire logic of the study. We cannot use good performance in a grasping task as indication of dorsal-stream involvement if DF performs just as well or even better in tasks that are assumed to be reliant on her impaired ventral stream. Finally, the data-set presented by Whitwell et al. (2014) is not consistent. Depending on the object used and the performance measures employed qualitatively different results were obtained. In short, Whitwell et al.'s (2014) findings cannot be used to support or reject either the calibration or the touch hypothesis.

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[4] Please note that the same critique also applies to a study by Rossit et al. (2011). Rossit and colleagues examined the grasping performance of a patient suffering from unilateral neglect. Immediate and delayed grasping movements were compared. The patient was impaired in the delayed but not in the immediate condition. As in the study by Goodale et al. (1994), the target object was removed at the onset of the delay interval. This meant that participants grasped a real object and received haptic feedback in the immediate condition but not in the delayed condition. Thus, again it may have been the lack of haptic feedback rather than the need to memorize the visual size of the object that caused the neglect patient's impaired grasping performance. This explanation is further supported by findings from our recent study (Utz et al., 2017) demonstrating neglect patients' increased reliance on sensory feedback even for visuomotor task where the visual target does not have to be memorized.

stands refuted as soon as a single convincing and contradicting instance has been demonstrated. The second reason relates to the fact that techniques used to remove visual target information frequently interfere with the availability of other sensory information that participants typically use in guiding their actions. Accordingly, we cannot be sure that it is actually the withdrawal of visual target information that accounts for the compromised performance. We already mentioned haptic feedback as one source of sensory information that is available in real-time action tasks but has usually been withdrawn in delayed-action experiments (see for example: Goodale et al., 1994a; Rossit, Fraser, Teasell, Malhotra, & Goodale, 2011).

Another source of information that differs between full-vision and delay conditions is the availability of visual feedback. The ability to see one's hand during reaching and grasping and to compare the hand position relative to the target position has been found to greatly and reliably improve the accuracy of the action (Hesse & Franz, 2009; Jakobson & Goodale, 1991; Westwood, Heath, et al., 2001; Wing, Turton, & Fraser, 1986). In fact, Hesse and Franz (2009) showed that movements are considerably less accurate when vision is occluded at movement onset (open-loop) as compared to full vision conditions (closed-loop), while further delays up to 5 sec have comparably smaller effects. In a recent study, we also showed that the availability of visual feedback might explain why neglect patients were found to consistently perform worse in anti-pointing tasks (i.e., task that requires them to point to a mirror-symmetric position of a presented target) as compared to standard pro-pointing tasks (Utz et al., 2017). That is, whenever patients were able to see both their hand and the target, they perform better in pro-pointing tasks as compared to anti-pointing tasks. However, this difference in performance between the two tasks disappeared when visual feedback was occluded suggesting that visual feedback can be used effectively to correct pro-pointing movements but not anti-pointing movements. This is quite unsurprising as visual feedback during pro-pointing allows us to compare the visual target position with the intended movement position and to use any discrepancy to correct potential movement errors (Saunders & Knill, 2003; 2005, see also Section 4). In contrast, the two locations are spatially dissociated in anti-pointing and hence there is no informative error signal. Importantly, these findings are of specific relevance for interpreting the observation that neglect patients were found to show impaired performance for delayed but not for immediate pointing compared to healthy control subjects (Rossit et al., 2009). If we assume that visual feedback is used to correct pointing movements in the closed-loop condition but is unavailable after delay this could potentially explain why neglect patients show normal performance in immediate pointing tasks and impaired performance in delayed pointing tasks. In short, we would argue that given that neglect patients produce significant errors when visual feedback is unavailable (Utz et al., 2017), normal performance can only be expected when effective error-correcting strategies are available (i.e., during closed-loop pro-pointing).

Similarly, another final potentially confounding factor that is relevant in this context is the availability of environmental information. Regarding the finding that DF shows impaired performance in delayed pointing and eye-movement tasks, we recently found some indication that this impairment may partly relate to the fact that she is unable to use environmental (landmark) information as efficiently as healthy participants. Visual landmarks are important cues in spatial visual memory tasks (Burgess, Spiers, & Paleologou, 2004). They can, however, only be effectively used when the relevant objects and their positions can be coded relative to them. This type of coding, called scene-based or allocentric visual coding, is impaired in DF (Dijkerman, Milner, & Carey, 1998; Schenk, 2006). It is therefore possible that DF's poor performance in some delayed-action tasks might reflect an inability to use landmarks rather than an inability to retrieve target information from visual memory. We recently found evidence to support this interpretation. Specifically, we observed that if landmark information was available during and after the delay period DF's performance was indeed worse than that of control participants. In contrast, she performed equally well as control participants in delay conditions where only egocentric information was available (Hesse & Schenk, 2014).

In summary, we argue that neuropsychological studies suggesting dissociations between delayed and immediate actions are inconclusive since the interventions used to introduce a delay also interfered with other sensory information relevant for accurate motor performance. In addition, finding that patient DF, a patient with extensive ventral stream damage, is still able to produce normal visuomotor performance under delay-conditions provides a serious challenge to the dorsal amnesia hypothesis and its claim that no normal memory-based visuomotor action is possible without an intact ventral stream.

Does this mean that we should abandon the dorsal amnesia hypothesis? This might seem too hasty at this point. There is still the puzzling finding of the delay-induced paradoxical improvement in patients with optic ataxia. As we noted above, this is a finding that is not predicted by any other model or hypothesis, and so far it seems that only the dorsal amnesia hypothesis can provide a satisfactory explanation for it. In the next section, we will summarize and critically discuss the findings on paradoxical improvement in optic ataxia.

3. Stuck in the past: how dorsal-stream damage affects memory-based action

Optic ataxia is a comparatively rare but very interesting and to some extent puzzling disorder. First described by Bálint (1909) it forms part of the so-called Balint-Holmes syndrome which is sometimes observed in the context of neuronal damage to posterior portions of the parietal cortex (Goethals & Santens, 2001). This type of neuronal damage can occur as a result of stroke but also in the course of neurodegenerative disorders such as posterior cortical atrophy, a form of dementia. Patients with Balint-Holmes syndrome have a narrow and restricted attentional field. As a result, they will find it difficult to appreciate the visual context in pictures, typically focussing on local features and thereby ignoring the global form of a line drawing (Goethals & Santens, 2001; Kerkhoff & Heldmann,

1999). Furthermore, they will misreach when aiming for visual targets. It is this last symptom that is referred to by the term "optic ataxia". Optic ataxia can be found in isolation, and it has been reported after unilateral or bilateral damage to the posterior parietal cortex. Very few cases show signs of misreaching when they are allowed to move their eyes freely and to directly gaze at a target object. Instead it is much more typical that the problems are restricted to conditions where the patient has to look at one position while reaching for a target presented at a different position and hence in visual periphery (Perenin & Vighetto, 1988). In fact, Borchers and colleagues argued that this aspect of optic ataxia (misreaching in visual periphery) is the most reliable criterion to distinguish optic ataxia from other motor disorders (Borchers et al., 2013). As the severity of the problems can depend on the tested hemifield (left or right) and the tested arm (left *vs* right), optic ataxia is a disorder which seems neither perceptual nor motor but a disorder of transforming visual input into motor output. It is thus considered to be a paradigmatic visuomotor disorder. Given this description, it is hardly surprising that the perception-action model presents optic ataxia as a representative example of dorsal stream damage (Milner & Goodale, 1995). Optic ataxia therefore provides the perfect opportunity to test the dorsal amnesia hypothesis.

According to the dorsal amnesia hypothesis, information about the visual target in the dorsal stream decays rapidly after the target has been removed from sight (Goodale, Króliczak, & Westwood, 2005, p. 273; Milner & Goodale, 2006, pp. 173, 174, 245ff). In optic ataxia the dorsal stream is damaged and the information in the dorsal stream is therefore compromised. However, when information in the dorsal stream is unavailable after delay, the motor system will take its visual input from the ventral stream that maintains visual representations for longer time periods (Milner & Goodale, 2006, p. 246). The ventral stream is preserved in optic ataxia and consequently its visual representations are available for action guidance. Thus, it can be expected that patients with optic ataxia will perform significantly better when they respond to memorized target information. Milner and his colleagues tested this idea in several studies and confirmed the prediction both for reaching and grasping behaviour (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Milner et al., 2001; Milner, Paulignan, et al., 1999). However, they pushed their hypothesis one step further.

If patients suffering from optic ataxia become reliant on stored visual information from the ventral stream, they might in fact use this stored information even when more current information is available. In one study which tested this prediction, the patient was asked to grasp an object; one object was presented at the start of the trial, vision of the object was then occluded for a few seconds, after which vision was restored such that the patient was again able to see a target and was prompted to reach forward and grasp it. In one condition, the object presented after the delay period was identical to the one presented before (same-condition) whereas in a second condition, a new object was placed in front of the patient (different condition). This new object could either be smaller or bigger than the one which was seen at the beginning of the trial. This study produced two interesting observations: Firstly, performance in the same condition was better than in a standard grasping task even though in both conditions the current target object was right in front of the patient's eyes at the time the grasping movement was initiated. Secondly, when a new object was presented after the delay period, the patient still seemed to adjust his grip to the size of the old object rather than to the size of the new and current target object (Milner et al., 2003; Milner, Paulignan, et al., 1999). Both observations seemed to confirm the idea that patients with optic ataxia are somehow stuck in the past and rely for their visuomotor behaviour on stored visual information, even when more current and relevant visual information is available. Taken together, these studies seem to demonstrate in a remarkable way that the perception-action model, and more specifically the dorsal amnesia hypothesis, inspires some interesting questions and is able to correctly predict some truly unexpected findings.

Importantly, it appears that only the perception-action model can provide a satisfactory explanation for those remarkable findings. Proponents of the perception-action model, therefore, challenge their critics to come up with alternative accounts − accounts which do not include the assumption of distinct pathways for perception and action (Westwood & Goodale, 2011). However, in our opinion, this is only a fair and relevant challenge if the perception-action model itself provides a satisfactory account for these observations. If this is not the case, these observations favour neither the proponents' nor the critics' view and are therefore irrelevant to the debate. Thus, the important question to ask here is whether or not the perception-action model can explain why patients with optic ataxia perform better after delay and why they seem to be stuck in the past when using visual information for action guidance?

Let us first look at the *stuck-in-the-past findings* and in particular at the condition where the objects prior and after delay are identical. The patient's performance in this task is better than when he is asked to grasp the object immediately without a delay. Is this really the behaviour that would be predicted by the dorsal amnesia hypothesis? The short answer needs to be: "No". The original version of the dorsal amnesia hypothesis predicts that a switch to ventral stream input, and thus paradoxical improvement for the patient, occurs when at the time of movement initiation no concurrent visual information is available. The patient, however, showed improvement in the presence of concurrent visual information. Milner et al. (2001) argued that in this condition the system will choose to pick the memorized information because it comes from the ventral stream, and will therefore be unaffected by dorsal damage. However, if the system has the capability to choose which visual information to use for action guidance why does it not exercise this capability also in the immediate grasping condition using the visual information from the intact ventral rather than from the damaged dorsal system? This assumption of the system's ability to choose visual information on the basis of expected informational quality becomes even more problematic when we consider the performance of the patient in the condition where two different objects are presented before and after the delay. In this condition, the patient seems to base his motor response on outdated memorised information and adjusts his grip to the earlier object. Thus, the patient uses information

that is clearly less accurate than the information presently available in both the dorsal and ventral stream areas. This is truly surprising behaviour and it should also be surprising to the proponents of the perception-action model. Firstly, if the absence of available visual information in the dorsal stream triggers the switch to ventral stream input for action guidance there should be no switch when concurrent visual information is available. If, however, the switch to ventral stream input is based on informational quality, then we would expect that the system would use the ventral visual information about the current object and not information about the no longer relevant earlier object. Thus, under both assumptions it is hard to understand why the patient's performance is affected by outdated object information.

The difficulty to accommodate the *stuck-in-the-past finding* within the perception-action framework becomes yet clearer when we contrast two possible explanatory scenarios. It seems clear that the patient's grasp after the delay reflects the target information from before the delay. This reliance on outdated visual information presented before the delay can be explained in two different ways. Either the motor act is prepared *after* the delay but instead of using the current information, stored visual information from before the delay is used. Or alternatively, the motor act could be prepared before the delay and not be updated at the time of movement initiation. Both scenarios result in the same outcome: the resulting motor response is adjusted to visual information from the previous object. Thus, both scenarios could in principle explain the *stuck-in-the-past* finding. In the following, we will argue that regardless of which scenario is considered, problems for the dorsal amnesia hypothesis arise.

The first option ("*prepare later but retrieve from before*") seems rather unlikely. In this scenario, the motor act is prepared when both new relevant and old outdated information are available. Why should the system retrieve outdated and irrelevant visual information when new and relevant information is available in both the ventral and the dorsal pathways? And if the system of the patient with optic ataxia has no choice in that matter and is destined to only ever use outdated information from visual memory shouldn't this reliance on stored information also be observed in other situations? For example, would it not be expected that the reaching and grasping behaviour in standard experiments without delays reflects the position or object size from the previous trial and not that from the current trial? Clearly this is not what has been found. At least for reaching behaviour it is obvious that the reach reflects the current target position, albeit imperfectly, and not the target position from a previous trial. A glance at the findings from a number of studies on patients with optic ataxia confirms that while these patients make significant errors — and typically errors that increase with the eccentricity of the visual target — the target position and reaching position are nevertheless well correlated (see for example, Himmelbach & Karnath, 2005; Perenin & Vighetto, 1988). Such a close quantitative relationship between target and movement is unlikely to emerge if in a randomized sequence of trials the current response of the patients was in fact linked to the target of the previous trial. To put it bluntly the "*prepare later but retrieve from before*" account is implausible and contradicts other findings from optic ataxia patients.

Let us therefore turn to the second possible account ("*prepare earlier but fail to update*"). According to this account, the patient prepares the motor act when the first object is presented. This motor act is then stored during the delay period. When, after the delay, the new object is presented the patient fails to notice the difference and consequently executes an action based on outdated visual information. This option avoids the problems of the first account. Moreover, it is a plausible account given that there is evidence for patients with optic ataxia failing to update ongoing visuomotor acts on the basis of new and action-relevant information (Pisella et al., 2000). On the basis of the second account, it is also easier to understand why optic ataxia patients may fail to update a motor act in a delayed reaching task but are still able to direct their next movement to a novel target and not to the target of the previous trial in a standard non-delayed reaching task. The assumption is that the execution of the prepared movement will bring the whole sensorimotor process to its natural conclusion, and for the next trial the system will start the process of motor preparation anew. Considering all this, the second account seems more plausible and more consistent with available empirical evidence. Nevertheless, it carries an implication which undermines the conventional logic underlying the dorsal amnesia hypothesis and its predictions. The stored-motor-act account implies that prepared motor acts can and will be stored when a delay is introduced between target presentation and response initiation. This means that the motor system does not have to refer back to the content of the ventral stream's visual memory to bridge the delay, instead it relies on a stored motor act that has already been prepared on the basis of visual information presented before the delay. Hence, within this framework, delayed actions would not be more reliant on ventral stream input than non-delayed actions. Accordingly, an improvement of movements performed by patients with optic ataxia after delay would ironically no longer be expected or predicted.

Thus, upon detailed analysis, the stuck-in-the past finding appears to be rather hard to reconcile with the perception-action model. In fact, the proponents of the model seem to be faced with an unattractive choice between an implausible account with implications contradicted by the patients' everyday behaviour and a more plausible account that undermines the very logic previously used in support of the dorsal amnesia hypothesis. Moreover, the stuck-in-the past finding is not the only problem for the dorsal amnesia hypothesis in the context of optic ataxia. This hypothesis assumes that actions are based on visual information from the dorsal stream if and only if vision is available at the time the movement is programmed (Goodale et al., 2005). Hence, it is expected that if neurologically healthy participants or patients with dorsal stream lesions execute actions after a delay, these should be based completely on visual information coming from the ventral stream. Consequently, visuomotor performance of patients with dorsal stream damage should be no worse and no better than the performance of healthy participants operating under the same delayed condition. Again this is not what has been found. In those studies where paradoxical improvements in delay conditions were observed, the performance of patients with optic ataxia after delay was mostly improved (but not always, see for example Khan et al.,

2005) but never came near normal performance (see for example Himmelbach et al., 2009; Milner, Paulignan, et al., 1999). Furthermore, the performance pattern found in another patient with optic ataxia after right-hemispheric lesion was decidedly mixed with regard to how delay affected movement accuracy (Revol et al., 2003). The effect of delay on behaviour depended on both the hemifield tested and the performance measure adopted. Delay reduced the variable error in the left visual hemifield but not the right. More importantly, while the variable error was reduced by delay in some conditions, the amplitude error was increased by delay in most conditions (Revol et al., 2003). It is not obvious how the dorsal amnesia hypothesis can account for this combination of results.

So the question arises if maybe the modified dorsal amnesia hypothesis as suggested by Singhal et al. (2013) fares any better. This is not at all clear. With respect to the delay-induced paradoxical improvement, it is not even clear whether such an improvement would be predicted by the modified version given the underlying assumption that during delay ventral stream input is injected into a damaged dorsal stream. In fact, it is difficult to derive predictions without specifying more precisely how the ventral and dorsal-stream processes interact during a delayed-action condition, and how this interaction is affected by dorsal stream damage. With respect to the *stuck-in-the past finding* we can be more specific. It is clear that the dorsal-amnesia modification as suggested by Singhal et al. (2013) contains no provision that allows it to explain why patients with optic ataxia recruit outdated information from visual memory when more recent information is available in both ventral and dorsal stream areas.

In summary, the surprising behaviour that patients with optic ataxia show when asked to interact with memorized visual targets cannot be used to support the dorsal amnesia hypothesis as it turns out that the findings, when looked at in more detail, are actually inconsistent with the assumptions and predictions of the perception-action model.

So far, we have focused on neuroscientific and neuropsychological evidence for the dorsal-amnesia hypothesis. However, there is also a large body of research on the relationship between visual memory and action control in healthy individuals. Some of those findings predated the advent of the perception-action model by several years and probably contributed to the adoption of the dorsal amnesia hypothesis as part of the perception-action model. In the following, we want to briefly review whether the evidence obtained from healthy individuals requires the dorsal amnesia hypothesis or whether it can be explained without recourse to the two-visual pathway hypothesis.

4. Dorsal amnesia: how reliance on memory impairs actions in neurologically intact humans

An interesting consequence of the formulation of the perception-action model (Goodale & Milner, 1992; Milner & Goodale, 1995, 2006) was an increased arousal of interest in the investigation of the relationship between visual factors and manual control, a topic that had been until then largely neglected by psychologists (see, Rosenbaum, 2005). Interestingly, however, it is often ignored that the question of how humans use visual information to control voluntary movements has been raised by a number of researchers well before the perception-action model was first formulated (e.g., Bowditch & Southard, 1882; Elliott & Allard, 1985; Elliott & Madalena, 1987; Thomson, 1980, 1983; Woodworth, 1899). In his now classic studies Woodworth (1899) could show that visually-guided hand movements (consisting of drawing lines of different lengths) get more inaccurate when they have to be performed very quickly. In contrast, when movements were made with the eyes shut, the correlation between speed and accuracy was absent with errors staying at a similar and relatively high level throughout different movement speeds. Woodworth suggested that goal-directed hand movements consistent of two successive phases: 1) the initial adjustment, which is ballistic and largely unaffected by the availability of visual information and 2) the phase of current control in which visual feedback is used to reduce the end-point error towards the end of the movement. Hence, the higher inaccuracy for visually-guided movements performed at high speeds was attributed to the fact that speed interfered with the current control phase, thus preventing finer adjustments in the end phase of the movement. In contrast, if movements are performed with the eyes shut, they rely primarily on the phase of initial adjustment (driven by the kinaesthetic sense) while no current control, based on visual information, can occur. Even though Woodworth (1899) already speculated that movements performed in the absence of vision may rely to some extent on visual memory of the target location, the spatial and temporal properties of these underlying visual representations were not systematically investigated until about 80 years later (Thomson, 1980, 1983).

In his studies, Thomson investigated how humans use visual information to control locomotion. In a series of experiments, he varied the length of the time interval between the occlusion of vision and reaching a target. He could show that accurate guidance (over longer distances) was possible for about 8 s after visual occlusion. After this critical time interval, performance was observed to deteriorate rapidly. Thomson hypothesised that movements were based upon an internal (most likely visual) image of the environment being available for a limited amount of time before fading out of short-term memory. However, a short-coming of these walking experiments was that walking distance and the time needed to reach the target were confounded (the issue was partly addressed by introducing conditions in which participants had to run to the target hence covering a larger distance in shorter time). Furthermore, a later study by Elliott (1986) failed to replicate Thomson's findings, instead suggesting that humans may rely on continuous visual information to control their movements accurately. In order to address this inconsistency between studies, Elliot and colleagues conducted a series of experiments systematically investigating the effect of delay on goal-directed reaching movements (e.g., Elliott & Lee, 1995; Elliott & Madalena, 1987; Elliott, Calvert, Jaeger, & Jones, 1990; Elliott, Carson, Goodman, & Chua, 1991).

In line with previous studies (Elliott & Allard, 1985; Keele & Posner, 1968; Zelaznik, Hawkins, & Kisselburgh, 1983), Elliott and Madalena (1987) observed that the pointing error

increased in conditions in which no visual feedback of the hand and the target was available (open-loop) as compared to conditions in which movements were performed with full visual feedback (closed-loop). Strikingly, however, accuracy deteriorated considerably when a 2 s delay was introduced while the effect of longer delays (up to 10 s) was comparably negligible (see also, Heath & Binsted, 2007; Heath & Westwood, 2003). Based on their finding, they suggested that in the absence of direct visual input a relatively accurate visual representation of the environment, contained in some kind of visual (iconic) memory, persists for a period of up to 2 s after visual occlusion. Even though Elliott and colleagues later stated that the visual presentation underlying the control of rapid limb movements may decay continuously and more rapidly than originally assumed (Elliott & Calvert, 1990; Elliott et al., 1990), the exact decay characteristics remained unclear.

Interestingly, the suggestion that accurate visual representations are available for up to 2 s after visual occlusion was initially adopted by the perception-action model (Hu, Eagleson, & Goodale, 1999; Milner & Goodale, 1995; Milner, Paulignan, et al., 1999). The proponents of the perception-action model, however, linked the finding that movement kinematics change considerably (less accurate and more variable) when delayed actions are performed to the idea that these movements do not rely on a current visual representation processed by the visuomotor mechanisms of the dorsal stream but rely instead on a stored visual representation of the object and its location which is processed by the perceptual mechanisms of the ventral stream. Yet again, none of these studies systematically examined the time frame over which the visual representations used to program the movements decayed (i.e., all studies applied delays of more than 2 s). The issue of how visual information used for movement programming decays during the first 2 sec of visual occlusion was first addressed in a series of experiments by Westwood and colleagues (Heath, Westwood, & Binsted, 2004; Westwood, Heath, et al., 2001; Westwood, Heath, & Roy, 2003). In one of their first studies in which Westwood, Heath, et al. (2001) investigated the accuracy of reaching movements after brief pre-response delays (durations of 500 msec, 1000 msec, 1500 msec and 2000 msec), they could show that the radial error was significantly larger whenever a delayed movement was required (as compared to closed-loop and open-loop reaching). Remarkably, the length of the delay had no effect on the pointing error suggesting that even after only 500 msec movements were programmed based on the stored (and less accurate but more durable) perceptual representation. More importantly, in a follow-up study, Westwood et al. (2003) introduced a "brief-delay" condition in which vision of the target and the moving hand was occluded simultaneously with the go-signal that signalled participants to start their movements. That is, the difference between the brief-delay condition and the classical open-loop condition (in which vision is usually occluded at movement onset) was just in whether or not participants were able to perceive the target during the movement programming phase (reaction time interval). The finding that movement kinematics in the brief delay condition were significantly different to those in the open-loop condition (and resembled movements performed after longer delays; see also Heath and Binsted (2007)) led the

authors to the conclusion that the visuomotor system operates in real-time. Hence, these studies formed the basis and first (behavioural) evidence for the notion that dorsal stream information is only used to support movement programming when direct visual input is available at the time of movement planning. In the absence of direct visual input, movements were assumed to rely on the stored representations of the environment maintained within the perceptual networks of the ventral pathway (*real-time hypothesis of motor programming*). In other words, according to this view, the visuomotor system does not store any target information at all and has no access to highly accurate information about the environment for *any time* following visual occlusion.

Given that the real-time hypothesis suggests that there is an immediate change in the processing mechanisms underlying the visuomotor control of our actions following visual occlusion, one would assume that the transition from one source of information (dorsal) to another (ventral) will become apparent in a sudden step-wise increase in movement errors. Specifically, the real-time hypothesis would predict that movement programming is based on accurate real-time information as long as the target is visible until movement initiation. Thus, movements performed in closed-loop and open-loop conditions should be of similar accuracy. Overall, a review of the literature reveals that findings are mixed, with the majority of studies showing that the elimination of visual feedback at movement onset strongly affects reaching and grasping kinematics (e.g., Elliott & Calvert, 1990; Franz, Hesse, & Kollath, 2009; Hesse & Franz, 2009, 2010; Jakobson & Goodale, 1991) while other studies suggest that it has no or only very little effect (e.g., Hu et al., 1999; Jeannerod, 1984; Winges, Weber, & Santello, 2003).

Furthermore, and more importantly, the real-time hypothesis predicts that movement kinematics change considerably between conditions in which either vision is available during movement initiation (open-loop after movement initiation [OL-Move]) or in which vision is occluded simultaneously with the "go-signal" (open-loop after go-signal [OL-Signal]). There are only few studies that tested this prediction directly and again their findings are inconsistent. While some studies suggest, in line with the real-time hypothesis, that OL-Move and OL-Signal conditions are very different from each other, with OL-Signal conditions being very similar to conditions introducing longer delays (Heath & Binsted, 2007; Westwood et al., 2003), other studies suggest that there are only incremental changes between the two conditions which primarily reflect an extra 300−400 msec of decay of the visual representation used to guide the hand movement (Elliott & Calvert, 1990; Hesse & Franz, 2009, 2010). Also, in two of their earlier studies (investigating the effect of the Mueller-Lyer illusion on grasping), Westwood and colleagues (Westwood, Heath, & Roy, 2000; Westwood, McEachern, & Roy, 2001) argued that OL-Move grasping movements were actually very similar to OL-Signal movements but considerably different from movements observed in a closed-loop conditions thereby stressing the importance of online visual feedback processes.

It is important to mention at this point that the contribution of feedback processes to effective movement control has been a matter of considerable debate within the motor control

literature for a long time (for review see Desmurget & Grafton, 2003). Specifically the early observations that a) relatively accurate actions can be performed when no sensory feedback is available and b) feedback loops might be too slow to control (fast) movements efficiently (Beaubaton & Hay, 1986; Carlton, 1981; Keele & Posner, 1968; Zelaznik et al., 1983) have led to the view that our movements might, by and large, be controlled in a feedforward manner with sensory feedback loops having only limited influence towards the end of the movement (for review see Desmurget & Grafton, 2003). However, while it was soon agreed that, due to the inherent sensory delays, fast hand movements cannot be efficiently controlled by sensory feedback loops alone, it was also found that these movements are considerably more accurate when sensory information is available (e.g., Carlton, 1981; Ghez, Gordon, & Ghilardi, 1995) undermining the hypothesis that fast hand movements are primarily under pre-programmed (feedforward) control. Hence, neither a model based solely on feedback mechanisms nor one that relies exclusively on feedforward control seems able to adequately capture the underlying control processes. Currently, the prevailing assumption is that feedback and feedforward control are combined in a forward model (Desmurget & Grafton, 2000; Miall & Wolpert, 1996). In this model, the motor system has learnt the consequences of a certain motor command (efferent signal) and uses this information to predict the expected sensory feedback. The prediction is then stored until the sensory feedback information becomes available (bridging the time needed to process this information), and the predicted and sensory states can be compared. If there is a mismatch in this information, an error signal is produced which in turn is used to update the prediction, modulate the motor command accordingly, and also to recalibrate the internal model which is involved in the feedforward control of movements. The beauty of this model is that it makes feedback strategies viable also for faster movements and that the position of the limb can be corrected despite significant time delays in the processing of feedback signals. Regarding the functional anatomy of the process, it has been suggested that a forward model of the arm's dynamics is maintained within the posterior parietal cortex that is used to predict the final state of the movement (for review see Desmurget & Grafton, 2000, 2003). In particular, the posterior parietal cortex is supposed to be involved in the computation of the dynamic motor error obtained by comparing the predicted movement point with the actual current end-point through forward modelling. The resulting error signal is then sent to the cerebellum which converts this information into a corrective error command. These parietal-cerebellar circuits are currently assumed to play a major role in hand movement guidance (Blakemore & Sirigu, 2003; Mulliken & Andersen, 2009). In short we can conclude that while our understanding regarding the precise mechanism by which visual feedback improves motor behaviour has changed in recent years, the relevance of visual feedback for optimal motor control is in no doubt. This means that studies that confound the manipulation of delay with the availability of visual feedback cannot provide conclusive evidence on the impact of delays on movement accuracy. Disentangling feedback and delays is however not the only issue, another issue concerns the precise way in which the

length of the delay interval is expected to influence motor performance.

According to the real-time view, the length of the delay should have no major effects on movement accuracy as visual feedback is always unavailable and, most importantly, all delayed movements are programmed based on the perceptual and long-lasting representations maintained within the ventral stream. Regarding these delay-dependent changes in movement kinematics, the proponents of the real-time hypothesis do not make any strong predictions. In fact, it has been suggested that it is likely that the visual representation in the ventral stream is subject to a gradual and continuous decay process (Westwood et al., 2003). Generally, as discussed above, the literature seems to indicate that movement kinematics change quite considerably during the first 2 s after visual occlusion but only very little following longer delays (Bradshaw & Watt, 2002; Elliott & Madalena, 1987; Heath & Binsted, 2007). To sum up, a careful look at the available literature reveals that there are currently no studies published that investigate reaching and grasping movements to simple objects (non-illusory context) in all the, according to the real-time view, critical vision conditions (CL, OL-Move, OL-Signal, OL-Delay) and report findings that support *all* of the assumptions made by this hypothesis.

In fact, until now, the studies investigating either manual aiming (Elliott & Calvert, 1990; Heath et al., 2004) or grasping movements to simple objects (Hesse & Franz, 2009, 2010) in all four critical vision conditions seem to suggest a continuous but rapid decay of the underlying visual information but no clear qualitative change in movement kinematics dependent on whether or not vision of the target was available during movement initiation. Specifically, Hesse & Franz argued that the decay characteristics (i.e., increased variability and decreased accuracy) could be best described by an exponential decay function, similar to those described in classical memory research (e.g., Anderson & Tweney, 1997; Ebbinghaus, 1885; Loftus, Duncan, & Gehrig, 1992; Wickelgren, 1970). Additionally, there are two studies that try to qualify the decay functions of visual information using a continuous tapping task (Binsted, Rolheiser, & Chua, 2006; Rolheiser, Binsted, & Brownell, 2006). While the use of continuous tapping tasks requiring repetitive movements has the advantage that the information decay can be monitored continuously, the studies applying continuous movement paradigms did not test specifically for the distinct effects of occluding target visibility during the movement initiation phase. Furthermore, even though both studies employed a very similar paradigm, their results were contradictory. While Rolheiser et al. (2006) observed a linear increase in movement variability as soon as vision was occluded, Binsted et al. (2006) reported a plateau of maintained movement accuracy for about 2 s after visual occlusion followed by a second-order decay.

The studies discussed so far investigated how reaching and grasping movements performed to simple targets are affected by the introduction of a pre-response delay. Even though it has been argued that decreased accuracy and increased variability reflect a decay (or change) of the underlying visual representation used for movement programming, these studies cannot exclude the possibility that instead of visual information, motor information is decaying. That is, it would

be equally likely that during the preview period a movement plan is generated and stored for later execution. In this case, the deterioration observed with increasing delays would reflect the decay of the pre-prepared motor responses and not the decay of the visual input. To put it differently, the above findings indicating performance decrements with delays between target presentation and response initiation can only count in favour of the dorsal amnesia hypothesis if the performance decrements actually reflect visual decay and not motor decay. In the next section, we will discuss studies which tried to disentangle visual decay and motor decay in delayed movement execution. The methodological tool employed to track the source of visual information used in tasks with and without delays are perceptual illusions.

5. Visual illusions, actions and delays

Evidence for the suggestion that the altered movement kinematics after delay are indeed a result of degraded visual information comes from studies investigating the effect of visual illusion on reaching and grasping kinematics in different vision conditions (e.g., Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu & Goodale, 2000; Westwood & Goodale, 2003; Westwood et al., 2000; Westwood, McEachern, et al., 2001). In short, the rationale of these studies is that when vision is available during the movement (or at least during movement initiation) the movement is programmed based on the metrically accurate representation of the dorsal stream and hence undeceived by the illusion. In contrast, when a response delay is introduced the movement has to be programmed based on the stored perceptual representation of the ventral stream and is therefore susceptible to the illusion. Even though almost all studies consistently find an increased illusion effect in the delay conditions as compared to closed-loop or open-loop conditions, the findings are not in direct support of the real-time hypothesis. Most importantly, the real-time hypothesis would predict that movements are unaffected by the illusion when vision is available during movement initiation (OL-Move condition) but deceived by it when vision is occluded at the moment movement initiation is required (OL-Signal). However, while indeed some studies did not report illusion effects on visuomotor performance when vision was occluded at movement initiation (Hu & Goodale, 2000; Westwood & Goodale, 2003); most studies find reliably illusion effects also in the OL-Move condition (Franz, 2001; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Franz et al., 2009; Heath, Rival, Westwood, & Neely, 2005; Hesse, Franz, & Schenk, 2016; Kopiske et al., 2016; Westwood, McEachern, et al., 2001). Furthermore, even though illusion effects on actions are often found to be reduced as compared to perceptual judgements, numerous studies still observe small but reliable illusion effects on visuomotor performance, even in full vision conditions (Aglioti et al., 1995; Bruno, Bernardis, & Gentilucci, 2008; for metaanalysis, see; Bruno & Franz, 2009; Bruno, Knox, & de Grave, 2010; for review,; Franz & Gegenfurtner, 2008; Heath et al., 2005; Kopiske et al., 2016). Besides, the real-time hypothesis predicts that illusion effects should be similar for movements performed in OL-Signal conditions and delayed

conditions (both mediated by the ventral stream). The findings regarding this prediction are much more consistent and largely in support of this notion (Franz et al., 2009; Gentilucci et al., 1996; Westwood et al., 2000; Westwood, McEachern, et al., 2001). Interestingly, however, Franz et al. (2009) showed that illusion effects increase almost linearly the earlier vision is suppressed during movement execution. Based on their findings, they argued that the size of the illusion effect on grasping can be better explained by the availability of visual feedback during grasping than by a shift from dorsal to ventral stream control (for similar argument see, Mon-Williams & Bull, 2000; Post & Welch, 1996). According to their view, the fact that illusion effects are of similar size for movements performed in OL-Signal and delay conditions therefore simply reflects the fact that there is no opportunity for online corrections in both conditions. In line with this suggestion, it was recently reported by de Brouwer, Brenner, Medendorp, and Smeets (2014) that presentation time but not response delay determines the size of saccadic illusion effects in the Mueller-Lyer figure.

Last but not least, it should be noted, that over the last years it has repeatedly been argued that the apparent dissociation between perception (large illusion effects) and action (small or no illusion effects) may mainly be due to the numerous methodological differences between conditions (see, Dassonville & Bala, 2004; Franz, 2001; Franz & Gegenfurtner, 2008; Franz et al., 2009; Hesse, Franz, et al., 2016; Mon-Williams & Bull, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; Post & Welch, 1996; Smeets & Brenner, 2006; Smeets, Brenner, de Grave, & Cuijpers, 2002), therefore generally questioning the usefulness of the paradigm to investigate the temporal processing characteristics of the dorsal and the ventral stream.

Thus, to summarise, studies employing visual illusions as stimuli are of particular importance for testing the dorsal-amnesia hypothesis in neurologically intact participants as they provide an elegant way of testing whether the observed decrement in visuomotor performance after delay can be attributed to a switch to a less suited (i.e., ventral stream) source of visual information (following the rapid decay of the relevant visual information in the better suited dorsal stream), or indicates instead a decay of the underlying motor program. Only if it can convincingly be shown that visuomotor performance deteriorates because of a loss in the quality of the relevant visual information, the dorsal-amnesia hypothesis can potentially be validated. While, at a first glance, there seems unequivocal support for the prediction that delays enhance illusion effects on actions, a more careful review of the literature shows that these changes are not at all in line with the more specific assumption that the occurrence of illusion effects on actions depends on whether or not visual information is available during movement programming (i.e., real-time view of action control). Moreover, there are a) methodological issues, i.e., the fact that illusions seem to reliably affect actions also in full-vision conditions (and to a similar extent than perceptions) when conditions are carefully matched and results are correctly analysed (see Kopiske et al., 2016 for an in-depth discussion), and b) alternative explanations, i.e., the fact that the removal of visual feedback can explain the differences between memory conditions, that

challenge the idea that visual illusions provide a reliable tool to measure the influence of the ventral (perceptual) stream on action processing.

Therefore, it appears that evidence from illusion studies is also not suited to provide convincing support for the claim that visual information decays rapidly in dorsal stream thereby causing the presumed switch to the ventral stream as visual source for action guidance and consequently an observed deterioration in performance levels after delay. Hence, the question arises if there are alternative methods and measures that can be used to determine whether actions are primarily based on dorsal or ventral stream input after memory delay. One alternative approach that has been suggested in this context is to look at the distinction between allocentric and egocentric information processing more generally and independent of illusory context. In the following, we will briefly summarise some of the key findings of the studies on this topic and will argue that in these studies too there is no clear evidence for the suggestion that memory delays force an inevitable switch from a dorsal to a ventral information processing mode.

6. The role of allocentric and egocentric cues for the visual guidance of actions

The underlying assumption of why visual illusions affect movements performed after delay but not in real time is that, according to the perception-action model, the long-lasting information represented within the ventral stream maintains information in an allocentric frame of reference (taking the environmental context into account). In contrast, the real-time information maintained in the dorsal stream is supposed to be represented in an egocentric frame of reference (relative to the observer). Hence, visual illusions will affect visuomotor actions only if visuomotor programming is based on an allocentric representation, but not if it is based on an egocentric representation (see also, Bridgeman, Gemmer, Forsman, & Huemer, 2000). Considering that it is hotly debated whether or not the visual illusion paradigm is suitable for revealing differences in the processing of perceptual and visuomotor information, the question arises of how else it can be tested which reference frame is used for information processing. The easiest way of investigating the use of allocentric information for visuomotor guidance is to let participants perform movements in either complete darkness (only egocentric information available) or in the presence of visual landmark cues (such as a structured background providing an allocentric reference frame). Previous studies suggest that when movements are carried out in the presence of visual landmarks, humans use a combination of both allocentric and egocentric cues in order to perform as accurately as possible (Carrozzo, Stratta, McIntyre, & Lacquaniti, 2002; Conti & Beauboton, 1980; Lemay, Bertram, & Stelmach, 2004; Redon & Hay, 2005; Toni, Gentilucci, Jeannerod, & Decety, 1996). In line with the predictions of the perception-action model, studies further showed that the significance of allocentric cues for visuomotor control increases when a memory delay is introduced (Bridgeman, Peery, & Anand, 1997; Chen, Byrne, & Crawford, 2011; Hay & Redon, 2006; Krigolson & Heath, 2004; Obhi &

Goodale, 2005), especially if these cues are task-relevant (Fiehler, Wolf, Klinghammer, & Blohm, 2014). However, contrasting the idea that immediate actions are based on egocentric information only while delayed actions are based on allocentric information only, it was also observed that both open-loop reaches performed in real-time (OL-Move) as well as reaches performed after longer delays benefit from the availability of allocentric information provided either before (Obhi & Goodale, 2005) or during the pointing movement (Krigolson & Heath, 2004). Furthermore, Krigolson and Heath (2004) also reported that in the presence of visual landmarks closed-loop reaches remained more accurate than open-loop or delayed movements, signifying again the importance of visual feedback processes.

In short, all these studies provide strong evidence for the notion that both memory-guided and real-time movements make use of allocentric information if available. While memory-guided movements tend to profit more strongly from the availability of allocentric information — suggesting that the visual system gives indeed more weight to allocentric than to egocentric information as memory demands increase — there seems to be no evidence for a clear cut shift from the use of one kind of reference frame (egocentric) to the use of a different kind of reference frame (allocentric) depending on vision condition. Instead it seems that both memory-guided and real-time movements recruit the same spatial maps albeit with different weights given to different spatial cues. This point was also confirmed by Rogers, Smith, and Schenk (2009). They tested the claim that memory-guided and real-time movements are based on distinct visuospatial maps by using a visuospatial learning paradigm. Using such a paradigm, we can induce changes to a spatial map employed in one task, and then examine whether those modifications will also affect performance in a second task. If the answer is yes, it might be concluded that the two tasks use the same spatial maps. Rogers and colleagues used the prismatic-adaptation paradigm. Participants are asked to wear prismatic goggles which shift their view by a few degrees to one side, e.g., the right. Participants will then perform visually based tasks such as pointing to targets or grasping an object and will rapidly learn that they need to adjust their movements to successfully interact with their visual environment. When the goggles are removed participants will show for some time a typical error which is spatially opposite to the spatial shift introduced by the goggles. This so-called postprismatic adaptation error is taken as evidence for the presumed re-calibration of the visuospatial map that was used for the visuomotor behaviour during the adaptation period (for more details on the prismatic adaptation procedure, see Newport & Schenk, 2012). If memory-guided and real-time movements rely on separate maps, one might expect that the visuospatial recalibration that takes place when memory-guided actions are performed will not affect the map used for real-time actions and vice versa. Accordingly one would expect that prism adaptation effects obtained with memory-guided actions do not transfer to real-time actions and vice versa. However, contrary to these expectations a substantial transfer of prism adaptation effects between those two conditions was observed (Rogers et al., 2009). Thus, it appears that delayed and immediate movements share common visuospatial resources.

Thus, similar to the findings from the illusion studies, the empirical observations point to a more gradual transition in the use of the available visual information rather than to a sudden switch between representations and processing modes (i.e., dorsal to ventral). Additionally, according to the perception-action model, egocentric spatial information should neither be used nor be available at all when movements are performed after longer delays (based on perceptual information). In contrast to this notion, Fiehler, Schütz, and Henriques (2011) showed that reaching targets are encoded and updated in a gaze-dependent egocentric frame of reference even when movements were delayed for up to 12 s. Unfortunately, a shortcoming of this study was that movements had to be performed in complete darkness, thus preventing the generation of an allocentric representation. In a follow-up study, Schütz, Henriques, and Fiehler (2013) investigated if gaze centred spatial updating also occurs when delayed reaching movements are performed in the presence of visual landmarks. They found that gaze dependent reaching errors persisted in conditions with available landmarks even though they were reduced compared to a no-landmarks condition. Further supporting the notion that egocentric target information can be maintained for a considerable amount of time after the movement target is removed from view, Ball, Smith, Ellison, and Schenk (2009) reported that participants benefited from the availability of egocentric cues in a visual search task even after a delay of more than 2 s. They used the spatial priming paradigm of visual search where the repeated presentation of the search target at the same location will lead to reliable reduction of search time It was found that regardless of whether this position was coded in an allocentric or egocentric format the priming effect always survived delays of several seconds (Ball, Smith, Ellison, & Schenk, 2010; Ball et al., 2009). In conclusion, these findings are inconsistent with the idea that egocentric representations are highly transient. Thus, even though the allocentric information is likely to be weighted higher after delay, egocentric information still seems to be available to the visuomotor system. The conclusion is in line with previous studies suggesting that egocentric and allocentric information is combined for movement execution based on their relative reliabilities (Byrne & Crawford, 2010; McGuire & Sabes, 2009).

7.　　Summary and conclusions

In this article we focused on one specific aspect of the perception-action model, its claim of the transient nature of the visual information processed in the dorsal stream. This claim, which we called the dorsal amnesia hypothesis, led to some interesting predictions and findings and received support from a wide range of different scientific domains. In this review, we critically re-examined the evidence from those different domains. We come to the conclusion that neither the findings from functional imaging and non-human primate single-unit recordings, nor the findings from behavioural studies with neurological patients and neurologically-healthy participants provide compelling support for the dorsal amnesia hypothesis. However, there might be a different and more nuanced version of the dorsal-amnesia hypothesis that

deserves further consideration and investigation. This nuanced version would stipulate that the time-dependent decay of visual information might be different for different visual attributes and also depends on the format of the representation, with allocentric representations being less affected by time-dependent changes than egocentric representations (see Hesse, Miller, & Buckingham, 2016; Hesse & Schenk, 2014 for examples). Accordingly, one might expect that the mix of visual information used for a given visuomotor task might indeed depend on the time elapsed between the receipt of that information and the onset of the associated action. Consequently, it might be expected that some tasks will be more influenced by the delays than others. Evidence for such a time-dependent change in the contribution of different sensory attributes to action control has been provided by a number of studies (see for example, Byrne & Crawford, 2010; Schütz et al., 2013), but it is worth reiterating that the differences are gradual and relative, and not absolute.

Most importantly, the original version of the dorsal amnesia hypothesis is in our view no longer tenable. A hypothesis which postulates a ventral-stream with exclusive access to visual memory and a dorsal pathway without memory access, distinct pathways and distinct visual representations for delayed and non-delayed actions is hard to uphold in the face of evidence of neural activity maintained for several seconds in dorsal-stream areas (see section 1), evidence of preserved performance in delayed visuomotor action in spite of extensive ventral-stream damage (see section 2), and evidence that visual illusions affect both immediate and delayed actions (see section 4). Given that the dorsal amnesia hypothesis is an integral part of the perception-action model its dismissal has implications for the model in general.

We argued above that the dorsal-amnesia hypothesis deserves a special place in the perception-action framework for several reasons. Firstly, the hypothesis provides the most clear-cut behavioural criterion to distinguish between ventral and dorsal functions. As has been argued before, other criteria such as perception versus action, indirect versus direct action, planning versus programming, deliberate versus automatic are fraud with ambivalence and hard to apply to concrete tasks and experimental paradigms (see Schenk, 2010). In contrast, the distinction between delayed versus immediate action is clear and can be measured in milliseconds (see Westwood & Goodale, 2003). Thus, one might argue that the predictions of the dorsal-amnesia hypothesis provide strong tests of the model and it is therefore disappointing that the outcomes of these tests frequently fails to fall in line with the model's predictions. Dismissing the dorsal-amnesia hypothesis thus means depriving the model of its most clear-cut behavioural criterion for distinguishing between ventral and dorsal function, thereby blunting its capacity for providing falsifiable predictions.

There is a second reason for why the dorsal-amnesia hypothesis is of special relevance to the model. The hypothesis predicted a novel finding which apparently can only be explained within the framework of the perception-action model. It led to the discovery that patients with optic ataxia produce fewer errors when they have to point or reach for

memorised visual targets, and may adjust their visuomotor response to the properties of memorised targets even if a novel target is presented. We argued above that these are indeed puzzling findings, but we also showed that the findings still remain puzzling even when considered within the perception-action framework. This is important for two reasons: Firstly, it shows that one of the model's most impressive discoveries is in fact a challenge to the model and cannot be counted in its support. Secondly, our reinterpretation of the findings on optic ataxia undermines a critique directed at sceptics of the perception-action model. Westwood and Goodale (2011) argued that regardless of how we view the controversy on illusions and actions, the fact remains that no model rejecting the concept of functionally distinct visual pathways for perception and action can explain the neuropsychological evidence obtained on patients with ventral and dorsal stream damage. It was previously argued that this is not true in the case of patient DF (see Schenk, 2010). With respect to optic ataxia, we argue here that while it is currently true that no good explanation has been offered for some of the relevant findings, this explanatory shortcoming also applies to the perception-action model. Thus, we agree that some of the neuropsychological findings are challenging and still require a compelling explanation. We would, however, argue that this challenge applies to all neuropsychological researchers regardless of their theoretical persuasion. This means there is no reason to assume that a satisfactory account can only be found within the two-visual pathway framework.

The dorsal amnesia hypothesis has been one of the least challenged and most productive components of the perception-action model. In this review, we argue that this hypothesis in its original form is incompatible with a considerable number of findings and therefore provides little support for the perception-action model. As other central aspects of the model have been criticized as well (Franz & Gegenfurtner, 2008; Kopiske et al., 2016; Schenk & McIntosh, 2010; Schenk, Franz, & Bruno, 2011), it is questionable whether the perception-action model still provides sufficient explanatory value to be seen as a useful model of how the primate visual system is organized.

This leads us to the next question.[5] If we challenge the perception-action model, what model can we propose in its place? To some extent, most critical challenges to the model have already implied an alternative view. Whenever a certain piece of evidence for the perception-action model has been criticized, this critique always included an alternative account. Dassonville and Bala (2004), Franz and Gegenfurtner (2008), Schenk (2012a), Jackson et al. (2009), Hesse and Schenk (2013), Utz, Hesse, Aschenneller, and Schenk (2015), to name just a few studies, all proposed and confirmed factors that could account for the perception-action dissociations without assuming a division of labour between vision for

perception and vision for action. Implied in these critical papers is an alternative framework that assumed that the visual system is not divided into separate streams but consists of specialized cortical regions forming ad-hoc networks to generate task-specific behaviour (see Schenk, 2010; Schenk et al., 2011 for a more detailed description). However, not everybody is convinced by such an alternative framework (Westwood & Goodale, 2011). The problem seems to be that perception-action dissociations found in different contexts receive different explanations within the alternative framework. Given that the perception-action model manages to explain the same set of observations with just a few simple principles, an alternative view will only be seen as competitive if it replaces the assumptions of the perception-action model with a set of assumptions that is comparable in size and simplicity, and has the same explanatory reach. Is this requirement for an acceptable alternative view justified? In the following, we will argue that several issues are associated with this requirement: a valid demand that can be met, a misconception that needs to be resolved, and a hope that should guide our future research but not our response to valid criticism.

It is a valid demand that when two alternative accounts for the same observations are compared, the number and complexity of novel or additional assumptions needed for each account have to be considered. Everything else being the same, the more parsimonious account, i.e., the one with fewer assumptions, is preferred. It seems the perception-model is superior in this regard managing to explain a wide range of observations with only a few principles. However, this impression is deceptive. It is true that different mechanisms and concepts have been evoked by sceptics to explain the different instances of perception-action dissociations. However, the employed mechanisms and concepts, such as the benefit of sensory feedback (Hesse & Franz, 2010; Schenk, 2012a) or the need to calibrate measuring variables (Franz, Fahle, Bülthoff, & Gegenfurtner, 2001; Franz & Gegenfurtner, 2008; Hesse, Franz, et al., 2016), are well established and do not require novel assumptions. No other assumptions about brain organization or brain processes are implied or needed. Importantly, the alternative view can dispense with the very assumptions that define the perception-action model. Seen in this light, the alternative view seems to offer the more parsimonious framework. It should also be noted that parsimony is only one of several criteria used to judge the merit of scientific models. A successful alternative account is also expected to generate correct predictions. Such predictions were derived and confirmed for most of the studies that suggested alternative accounts. The study by Dassonville and Bala (2004) provides a good example. They looked at the induced Roelof illusion and the finding that this illusion affects anti-pointing but not pro-pointing. This dissociation was taken as evidence for the claim that illusions affect only tasks based on ventral stream processing (i.e., anti-pointing). Dassonville and Bala (2004) proposed an alternative hypothesis: The induced Roelof illusion shifts the perception of our subjective midpoint. They argued that such a midpoint shift will affect the spatial coding of the hand and the target. In pro-pointing, the two effects will cancel each other out. In anti-pointing, the shift in midpoint will affect both the computation of the distance

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[5] These final paragraphs were inspired by a comment from an anonymous reviewer who questioned the scientific merit of a review (such as ours) that criticizes an established model without offering suggestions for an alternative. Given that similar comments were frequently raised in the past, we decided it is time to provide a detailed answer to this challenge.

between visual target and midpoint, and the projection of that distance into opposite hemispace. As a result, the error in anti-pointing should be twice as big as the error measured with a perceptual matching task. This finding was confirmed in two independent labs. It illustrates that alternative accounts for the perception-action model generate novel findings not predicted by the perception-action model.

Nevertheless, we anticipate that there may still be researchers who are not convinced by this answer (see for example: Milner & Goodale, 2006, p. 241). We also suspect that those researchers wait for an alternative model that can meet stricter demands. They may expect a model which provides a common principle to explain the evidence on perceptual illusions, visual form agnosia and optic ataxia. However, what is it that the perception-action model explains about illusions, form agnosia and optic ataxia? The perception-action model explains neither of these phenomena per se, it primarily explains why dissociations between perceptual and visuomotor tasks occur in these domains. Thus, the only common feature linking those domains is the occurrence of perception-action dissociations. Provide alternative accounts for those dissociations and the link is lost. Outside of the theoretical framework of the perception-action model, visual illusions, visual form agnosia and optic ataxia have as much in common as for example, colour constancy, neglect and apraxia. Thus, it seems almost unavoidable that an alternative that replaces the perception-action principle with something else will destroy the link between illusions, agnosia and optic ataxia. Therefore, an alternative view should not be expected to provide a new link between those domains. The demand for a new principle providing a new link between those domains may also be motivated by the idea that it is easier to compare two scientific alternatives when both alternatives are based on one key hypothesis that aims to explain the same set of data. This seems to facilitate the application of the principle of parsimony. Given that two alternative models explain the exact same observations, the model containing the smallest number of assumptions is preferred. We concede that such a case provides an easy situation for selecting the best model based on parsimony. It is, however, wrong to demand that when judging parsimony, we restrict ourselves to the assumptions inherent to the core hypothesis. Parsimony has to be judged relative to the total sum of assumptions in a given scientific field. The account that provides the best explanatory fit with the least number of additional assumptions is the most parsimonious. In this calculation assumptions are not counted if they have already been established by earlier findings and form part of uncontroversial models or explanations. This means that an alternative that uses ten different well-established assumptions to explain a set of ten findings is still more parsimonious than a model that needs to introduce only one but one additional principle to account for those findings.

We would like to illustrate this point using a spoof theory: the colour-attraction model (CAM). Imagine that someone suggests that objects of similar colour attract each other. As evidence for this model the following findings are presented: Animals are frequently found on backgrounds that share their colour; in a rainbow similar colours are next to each other; in recycling containers glass bottles of the same colour are found

in the same container. It seems CAM explains findings from three different domains using just on simple principle. However, we know that the correct explanations are different. Camouflage explains why animals seek out backgrounds matching their own colour. Laws of optics explain the sequence of colours in the rainbow, and recycling laws are responsible for the sorting of bottles according to their colours. In this case, the correct explanations use more assumptions than CAM, use different assumptions for each of the three different observations, and do not provide an alternative, unifying principle. Yet, they are still the better explanations because their assumptions are already well-established, meaning that the CAM assumption is superfluous. This fictive example is not meant as persiflage of the perception-action model which we consider a useful scientific model. Nevertheless, the mock example serves our purpose. It shows that it is not necessarily justified to demand an alternative account which uses just one small set of coherent assumptions to explain a set of different observations previously associated with the perception-action model.

Behind the demand for an alternative model that replaces the assumptions of the perception-action model with another set of simple principles also lies a hope — the hope that some of the simplicity and order that the perception-action model imposed on the complex architecture of the primate visual system (Felleman & Van Essen, 1991) will eventually be restored. We share this hope and concede that the alternative view sketched out here and elsewhere (Schenk, 2010; Schenk et al., 2011) does not provide progress in this direction. We would, however, also insist that the business of examining the problems, describing the flaws and testing the implications of an established model can be done independently of the business of developing a detailed alternative account. A mandatory linking of the two, as is sometimes suggested, is in our view counterproductive. It sets the bar too high for valid criticism, stifles scientific debate, and if upheld as a general principle renders scientific models unproductive and thus hinders scientific progress.

Acknowledgements

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