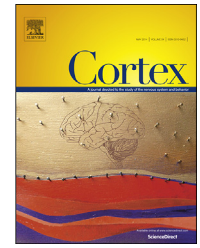
Available online at www.sciencedirect.com

ScienceDirect

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



Research report

Delayed action does not always require the ventral stream: A study on a patient with visual form agnosia

Constanze Hesse [a,*] *and Thomas Schenk* [b]

[a] *School of Psychology, University of Aberdeen, UK*
[b] *Neurology, University of Erlangen-Nuremberg, Germany*

ARTICLE INFO

Article history:
Received 26 June 2013
Reviewed 9 August 2013
Revised 14 October 2013
Accepted 12 February 2014
Action editor David Carey
Published online 22 February 2014

Keywords:
Perception–action model
Visual form agnosia
Delay
Posting
Patient D.F.

ABSTRACT

It has been suggested that while movements directed at visible targets are processed within the dorsal stream, movements executed after delay rely on the visual representations of the ventral stream (Milner & Goodale, 2006). This interpretation is supported by the observation that a patient with ventral stream damage (D.F.) has trouble performing accurate movements after a delay, but performs normally when the target is visible during movement programming. We tested D.F.'s visuomotor performance in a letter-posting task whilst varying the amount of visual feedback available. Additionally, we also varied whether D.F. received tactile feedback at the end of each trial (posting through a letter box *vs* posting on a screen) and whether environmental cues were available during the delay period (removing the target only *vs* suppressing vision completely with shutter glasses). We found that in the absence of environmental cues patient D.F. was unaffected by the introduction of delay and performed as accurately as healthy controls. However, when environmental cues and vision of the moving hand were available during and after the delay period, D.F.'s visuomotor performance was impaired. Thus, while healthy controls benefit from the availability of environmental landmarks and/or visual feedback of the moving hand, such cues seem less beneficial to D.F. Taken together our findings suggest that ventral stream damage does not always impact the ability to make delayed movements but compromises the ability to use environmental landmarks and visual feedback efficiently.

1. Introduction

The distinction between immediate and memory-guided actions plays an important role in Goodale and Milner's influential perception–action model (Goodale & Milner, 1992; Milner & Goodale, 1995; Milner & Goodale, 2006). According to this model, visual information is processed differently depending on the purpose for which the information is

* *Corresponding author*. School of Psychology, University of Aberdeen, King's Campus, Aberdeen AB24 3FX, UK.
E-mail address: c.hesse@abdn.ac.uk (C. Hesse).
http://dx.doi.org/10.1016/j.cortex.2014.02.011

acquired: In order to identify or recognise objects, information is processed within the ventral stream (vision for perception), whereas for the visual guidance of actions, information is processed within the dorsal stream (vision for action). In order to suit the different purposes of action and perception, it was suggested that both visual streams operate on different time scales (Goodale, Kroliczak, & Westwood, 2005; Goodale, Westwood, & Milner, 2004; Milner et al., 2001; Rossetti, 1998). For action planning, the relative position between target and observer has to be taken into account. Since in natural conditions observers are moving, these relative positions change constantly. Accordingly, it was proposed that information in the dorsal stream is not stored over longer periods of time. In contrast, for object identification and recognition, information in the ventral stream has to be stored independently of viewpoint over longer time spans. Following this argument, it was suggested that actions directed to visible targets are guided by the dorsal stream whereas actions executed after a delay (delayed actions or memory-guided actions) have to rely on ventral stream information, thus causing alterations in movement kinematics (Goodale et al., 2005, 2004; Hu, Eagleson, & Goodale, 1999; Westwood & Goodale, 2003; Westwood, Heath, & Roy, 2003).

Originally, it was assumed that visual information in the dorsal stream remains available for a maximum time of 2 sec (Goodale, Jakobson, & Keillor, 1994). However, more recently it has been suggested that the dorsal stream is in fact only engaged in movement programming if vision is available at the moment when the movement is initiated (Goodale et al., 2005; Goodale & Westwood, 2004; Goodale et al., 2004; Westwood & Goodale, 2003). According to this "real-time view of motor programming", action programming does not occur before the decision to move has been made. Specifically, it has been hypothesised that the dorsal stream can only supply the relevant visual information if this information is present on the retina during action programming. In other words, if visual information is unavailable during the programming phase of the movement, the action system has no access to dorsal input and instead has to rely on visual information from the ventral stream resulting in qualitatively different movements.

Recent research on the topic, primarily investigating grasping movements, has called this real-time view (i.e., the suggestion that the dorsal stream is amnestic) into question. The real-time view of action makes three clear predictions: (1) the kinematics of movements performed after delay will be considerably different from the kinematics of movements that are programmed whilst the target object is visible; (2) the introduction of a delay period will shift the neuronal activity from the dorsal to the ventral system; (3) damage to the ventral stream will selectively impair the patient's ability to carry out accurate movements after delay. The first prediction was examined by Hesse and Franz (2009, 2010) and they found that in healthy participants grasping kinematics did not change abruptly depending on whether visual information is present during the movement programming phase or not (Hesse & Franz, 2009, 2010). Instead, the authors suggested that there is a gradual (exponential) decay of visuomotor information over time (Hesse & Franz, 2010; for a different view see, Hu et al., 1999; Westwood, Heath, & Roy, 2001). The second prediction was examined in a number of functional imaging studies. These studies revealed that even after a delay of up to 12 sec, activity can be found in the dorsal stream area when simple reaching and grasping movements have to be performed (Connolly, Andersen, & Goodale, 2003; Fiehler et al., 2011; Himmelbach et al., 2009; Lacquaniti et al., 1997). Based on these findings, it has been suggested that the changes in movement kinematics after delay might be attributed to an information decay occurring in both visual streams (Hesse & Franz, 2009), or alternatively that there might be a much more gradual shift from dorsal to ventral processing over time (Himmelbach & Karnath, 2005).

What about the third prediction? The prediction that selective ventral stream damage will lead to a selective deficit of delayed actions was examined in patient D.F., who has sustained bilateral damage to her ventral stream (Milner et al., 1991). Until now, this prediction has received support from all relevant studies (Goodale et al., 1994; Milner, Dijkerman, & Carey, 1999; Milner & Goodale, 2006; Rossit, Szymanek, Butler, & Harvey, 2010). The observed dissociation between D.F.'s intact ability to perform immediate actions and her impaired ability to perform accurate delayed actions provides therefore the most compelling evidence for the assumption that the dorsal and the ventral streams work on different time scales. Hence, if we want to challenge the hypothesis that delayed actions critically depend on ventral stream processing, we need to provide an alternative explanation for the finding that D.F.'s visuomotor performance is impaired after delay.

In our alternative account we assume that visual information decays generally over time (no matter where it is represented) resulting in less accurate movements with longer delays (for similar view see also, Elliott, Calvert, Jaeger, & Jones, 1990). In particular, the memory decay will be associated with an increased uncertainty about the properties of the target object such as its position, size or orientation. Healthy participants are able to partly compensate for this information decay by using other available (sensory) information such as visual landmarks. Previous research suggests that the availability of visual landmarks facilitates not only visually-guided movements but also movements performed after delay (Conti & Beaubaton, 1980; Hay & Redon, 2006; Krigolson & Heath, 2004; Lemay, Bertram, & Stelmach, 2004). That is, if visual background information (for example, four illuminated light-emitting diodes (LEDs) positioned in a square surrounding the target locations) is presented, reaches are more accurate and less variable than in conditions in which the same targets are presented on an empty (dark) visual background (Krigolson & Heath, 2004). Based on these findings it was argued that the availability of contextual information surrounding a target (allocentric cues) in combination with vision of the moving limb (egocentric cues) considerably enhances the accuracy of (memory-guided) movements. In situations in which no environmental cues are provided, the only information available in order to point accurately is the remembered position of the target in relation to your own body (egocentric information). However, by providing visual landmarks during the delay period the target can be coded relative to these landmarks (e.g., about 10 cm to left of the LED). Coded this way, the target position can still be recalled accurately, even after a delay of a few seconds,