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Delay abolishes the obstacle avoidance deficit in unilateral optic ataxia

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Abstract

Optic ataxic patients have deficits in the visual control of manual reaching and grasping. It has been established previously that these deficits in target-directed behaviour improve following a delay in response. Recently it has been demonstrated that optic ataxic patients also have deficits in taking potential obstacles into account during reaching. The present study was therefore designed to test whether delay would bring an improvement in this behaviour as well. We present experimental data from a patient with unilateral optic ataxia (M.H.). First we document M.H.'s pointing errors, which show a reliable pattern of impairment when pointing to targets in his right visual field, particularly when using his right hand. We then show that a similar pattern of deficits is observable in his ability to negotiate between non-targets: that is, M.H. selectively fails to take account of obstacles in his *right* visual field, but only while reaching with his *right* hand. Finally we demonstrate that this obstacle avoidance deficit disappears following a 5 s delay in response: under these conditions M.H. now takes account of both non-target objects with either hand. The results are interpreted within the 'two visual streams' model of cortical visual processing.
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Keywords: Visuomotor behaviour; Optic ataxia; Reaching; Dorsal stream; Two visual systems

1. Introduction

Optic ataxia is traditionally defined as a disorder of accuracy in reaching towards a visual target (Bálint, 1909; translated into English by Harvey, 1995). In his original description of optic ataxia, Bálint noted that the inaccuracy of manual control seen in his patient was restricted to one hand (the right hand), despite the presence of bilateral parietal lesions. More recently, it has been shown that optic ataxia patients typically present a generalized disorder in the visual guidance of movement, including orienting and shaping the hand correctly in anticipation of contact with the object (Goodale, Meenan et al., 1994; Jakobson, Archibald, Carey, & Goodale, 1991; Jeannerod, 1986; Perenin & Vighetto, 1988). Perenin and Vighetto (1988) observed that optic ataxia following unilateral damage to the right hemisphere was generally characterized by deficits related only to the contralateral visual field, regardless of the hand used, whereas following damage to the left hemisphere it often also included deficits related to the contralateral hand.

More recent studies have confirmed these observations, and have also shown that optic ataxic deficits include both the programming (Ishihara et al., 2004; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003) and the on-line control (Gréa et al., 2002; Pisella et al., 2000) of target-directed reaching movements. In addition, it has recently been shown that the range of deficits in optic ataxia extends to the processing of non-target stimuli located in action space during reaching. Schindler et al. (2004) showed that two patients with bilateral optic ataxia failed completely to take account of the shifting locations of two potential obstacles in their workspace when they were required to

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reach between them. In contrast, both patients were able to take full account of the positions of the obstacles when they were required to indicate the mid-point between them in a perceptual bisection task. The research of Schindler et al. (2004) was conceived within the 'two visual streams' model put forward by Milner and Goodale (1995, 2006). That model proposes that the cortical ventral and dorsal visual streams separately underlie vision-for-perception and vision-for-action, respectively. More specifically, the ventral stream, projecting from striate cortex to inferotemporal cortex, mediates perception and recognition, whereas the dorsal stream, projecting from striate cortex to posterior parietal cortex, is involved in the control of action dynamics in real time. Schindler et al. (2004) concluded that obstacle avoidance requires the dorsal stream – since the system was damaged bilaterally in their two patients – whereas their bisection task depends primarily on the ventral visual stream (presumed intact in these patients). This interpretation was supported by a follow-up study showing that two patients with visual form agnosia, following bilateral ventral-stream damage, retained good obstacle avoidance despite showing deficits in the bisection task (Rice et al., 2006).

These recent data provide clear support for the idea that the dorsal stream subserves the visuomotor processing of non-targets as well as target objects. Given this conclusion, other questions immediately arise. Milner and Goodale (1995) argued that the two visual streams necessarily operate on different time scales. The dorsal stream works in real time, generating the required visuomotor co-ordinates for immediate use in guiding action. In contrast, a major role of the ventral stream is to provide the contents of visual memory, for later use in both the short and long term. In accordance with these ideas, it has been found that when the ventral stream is damaged, as in patient D.F., severe impairments in (otherwise normal) visuomotor control are induced when a very short delay is required before a reaching or grasping response is made (Goodale, Jakobson, & Keillor, 1994; Milner, Dijkerman, & Carey, 1999). It was argued that delayed responding requires ventral-stream processing, since this is the only means by which working memory can acquire perceptual content. In other words, under delayed conditions a ventral-stream route has to substitute for the direct dorsal-stream route, which is usable only in real time. In patient D.F., of course, the possibility of such re-routing via the ventral stream would not have been available, hence the impairment.

Milner, Paulignan, Dijkerman, Michel, and Jeannerod (1999) made the opposite, somewhat counter-intuitive, prediction for optic ataxia patients. They argued that the deficits in visuomotor control seen in these patients, caused by damage to the dorsal stream of processing, should be *ameliorated* when a delay was imposed prior to response. Since the delay should cause a shift to a dependence on visual processing in the ventral stream, which is generally intact in such patients, this might allow improved visuomotor performance. This prediction was confirmed using a pointing task (Milner, Paulignan et al., 1999), and the results have been replicated in other patients (Himmelbach & Karnath, 2005; Revol et al., 2003). In a further study Milner et al. (2001) were able to demonstrate a parallel improvement with delay in the visual calibration of grip size during a grasping task. Apparently then, although not ideally suited to the control of action, ventral-stream processing can provide an improvement in several aspects of visuomotor guidance in optic ataxia when actions are delayed.

In the present paper we present the results of experiments carried out with patient M.H., who developed optic ataxia following an anoxic episode. Behaviourally, M.H. showed an asymmetric pattern of reaching impairment in which performance was worst for stimuli in the right hemispace when he used his right hand. In Experiment 1, we report the pattern of hand and field deficits observed in M.H. when carrying out a simple pointing task. In Experiment 2, we tested whether the pattern of deficits seen in target-directed behaviour could be duplicated in his obstacle avoidance behaviour. Finally, in Experiment 3 we investigated whether a delay in response would help improve M.H.'s ability to take account of potential obstacles in the workspace.

2. Experiment 1: pointing

2.1. Method

2.1.1. Participant

Patient M.H. was 49 years old at the time of testing. The anoxic incident that caused his brain injury resulted in right side muscle weakness and raised sensory thresholds. He was still able to walk and use both hands, though he reported difficulties in everyday living activities, such as dressing, eating with a knife and fork, and writing. Clinical assessment showed no evidence of unilateral neglect or agraphia (see Riddoch et al., 2004, for further details). A recent MRI scan (2006) showed disseminated lesions consistent with the anoxic aetiology (see Fig. 1). Posterior parietal atrophy was present bilaterally, though more pronounced on the left, with an epicentre lying superiorly in the region of the intraparietal sulcus, and with some extension onto the medial aspect and into the inferior parietal lobule. Sub-cortical atrophy was apparent bilaterally in the lentiform nucleus and claustrum, and less marked atrophy was seen in the left frontal (chiefly premotor) and perisylvian (frontotemporal) regions. The occipital lobes were largely unaffected.

The University of Birmingham School of Psychology ethics committee approved the experiments described here, and informed consent was obtained prior to the study in accordance with the principles of the Declaration of Helsinki.

2.1.2. Experimental equipment

Patient M.H. was seated at a table on which a starting point (diameter 2 cm) was positioned on the mid-sagittal axis, 5 cm from the table edge. A target was presented at one of four possible locations, two on the left and two on the right, positioned symmetrical to the mid-sagittal axis. The target positions were 5 cm apart and lay along a line 20 cm from the starting point. The locations were faintly marked on the table so that a small red circle target (diameter 0.5 cm; paper thin) could be placed accurately in the same position throughout the experiment. Only one target object was presented at a time. At the opposite side of the table, 60 cm from the starting point along the sagittal axis,

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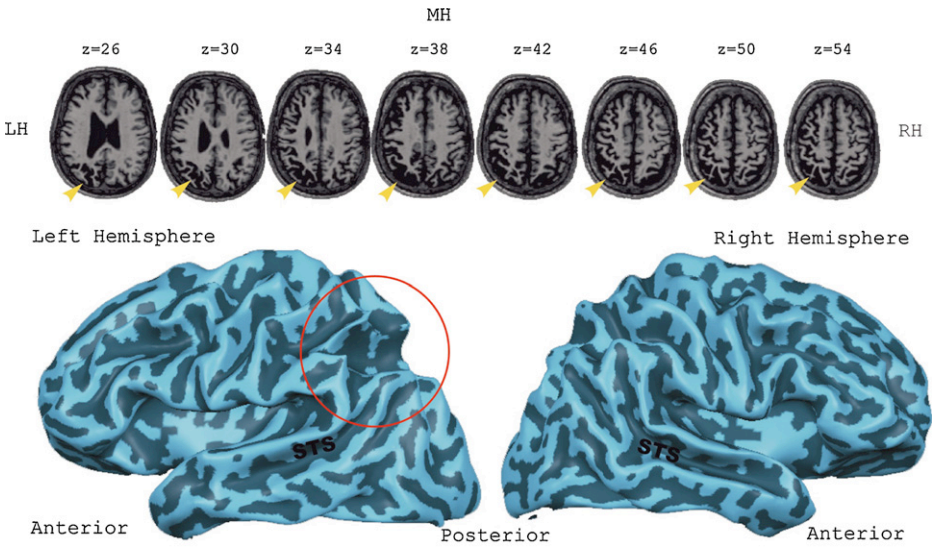

Fig. 1. MRI scan of M.H.'s lesion. Axial slices taken from the 3D anatomical MRI scan of patient M.H. ($z = 24$ to $z = 54$) showing the site of the lesion in the left parietal lobe with arrows (top panel). The cortical surface of M.H. was rendered in 3D using *Brain Voyager* QX 1.7 software (Brain Innovation, Maastricht, Netherlands) to produce inflated surfaces of the left and right hemispheres that exclude the lesioned brain matter. The site of the lesion is marked with a circle on the left inflated surface (bottom panel of Fig. 1). The location of the superior temporal sulcus (STS) is labeled on the inflated surfaces for reference.

a 2 cm diameter green circle was placed and used as a fixation point.

Movement kinematics were measured using a dual-camera *MacReflex* 50 Hz infrared 3D motion analysis tracking system with a mean accuracy of 0.1 mm. A single reflective marker (1 cm diameter) was attached to M.H.'s index fingernail using adhesive gel.

2.1.3. Procedure

M.H. was required to point to the target object with the left or right hand, and using central or peripheral vision (i.e., no fixation vs. fixation). Trials were run in blocks for the hand and vision conditions, with trials to each target randomized within each block. Each block consisted of four trials per target and each was run twice in a counterbalanced ABBA order (giving eight trials per trial type).

Before each block of trials, M.H. was instructed as to which hand to use and whether he was allowed to look at the target (central vision condition), or was required to fix his gaze on the fixation point (peripheral vision condition). Before each trial, M.H. was instructed to place his index finger on the start point, after which the experimenter positioned the target. A computer beep indicated the beginning of the trial, and M.H. was required to point to the target. During peripheral vision trials, the experimenter visually monitored the patient's eye position. If M.H.'s eyes moved, the trial was discarded, and repeated at the end of the trial block.

2.1.4. Analysis

A total of seven trials were removed from the data set as having values that were outside a 3-S.D. range from the mean. A factorial ANOVA was used to test the effects of hand (left vs. right), fixation condition (central vs. peripheral) and target position (left vs. right). Separate analyses were conducted for reach error (mm), reaction time (ms), movement time (ms), peak velocity (mm/s), and percentage time to reach peak velocity. Reach error was the Cartesian distance between the index finger's end position and the pre-calibrated target position. Reaction time was defined as the time after the start signal at which the velocity of the marker attached to index finger rose above 50 mm/s. Movement time was defined as the time after the start signal at which the velocity of the marker attached to the index finger fell below 50 mm/s, minus reaction time. Peak velocity was defined as the maximum velocity of the marker attached to index finger. Percentage time to peak velocity was the time after the start signal at which peak velocity occurred minus reaction time, expressed as a percentage of movement time. For conciseness, only significant findings are reported here. A significance threshold of 0.05 was used throughout.

2.2. Results

Analysis of reaching error revealed a significant effect of hand ($F_{1,113} = 33.66$, $p < 0.001$), fixation condition ($F_{1,113} = 156.09$, $p < 0.001$) and target position ($F_{1,113} = 37.2$, $p < 0.001$). These data show that M.H.'s performance was worse with his right than his left hand, worse in peripheral than central vision, and worse for right targets than for left (see Fig. 2). In addition, significant interactions were observed for hand × fixation ($F_{1,113} = 21.46$, $p < 0.001$), hand × position ($F_{1,113} = 9.09$, $p < 0.003$), fixation × position ($F_{1,113} = 38.19$, $p < 0.001$), and finally a significant interaction was observed between hand × fixation × position ($F_{1,113} = 7.733$, $p = 0.006$). As Fig. 2 clearly illustrates, this three-way effect is driven by the fact that M.H. showed greatest errors when using his right hand in his right field under peripheral stimulus conditions.

The kinematic data are presented in Table 1. For reaction time, we observed only a significant effect of fixation condition

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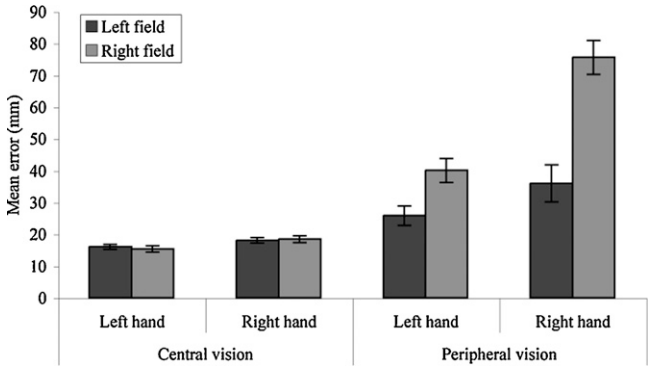

Fig. 2. Reaching errors in Experiment 1. Graph illustrates the mean (and standard error) of reaching errors with the left and right hand, in the left and right visual field, under central and peripheral reaching conditions. Largest errors are observed when M.H. reaches with his right hand in his right visual field (under peripheral viewing conditions).

($F_{1,113} = 152.00$, $p < 0.001$), with M.H. taking longer to initiate his response under peripheral vision conditions. For peak velocity a significant effect of hand ($F_{1,113} = 21.471$, $p < 0.001$) and fixation condition ($F_{1,113} = 126.67$, $p < 0.001$) were observed, with M.H. moving slower overall with his right hand and when using peripheral vision. An interaction was also observed between fixation × position ($F_{1,113} = 7.723$, $p = 0.006$). This effect reflects the fact that under central viewing M.H. moved faster to right-side targets, but under peripheral viewing he moved faster to left side targets. A consistent pattern of results was observed for movement time, where again significant effects of hand ($F_{1,113} = 19.134$, $p < 0.001$), fixation ($F_{1,113} = 34.18$, $p < 0.001$), and fixation × position ($F_{1,113} = 5.54$, $p = 0.022$), were found.

3. Experiment 2: immediate obstacle avoidance

3.1. Method

3.1.1. Participants

Patient M.H., aged 50 at the time of testing, and 8 healthy age-matched controls between 44 and 60 years of age, took part in this experiment. All control subjects were right handed by self-report, had normal or corrected-to-normal vision, and had no history of neurological disorder. Informed consent was obtained from each participant prior to participation in the study in accordance with the principles of the Declaration of Helsinki.

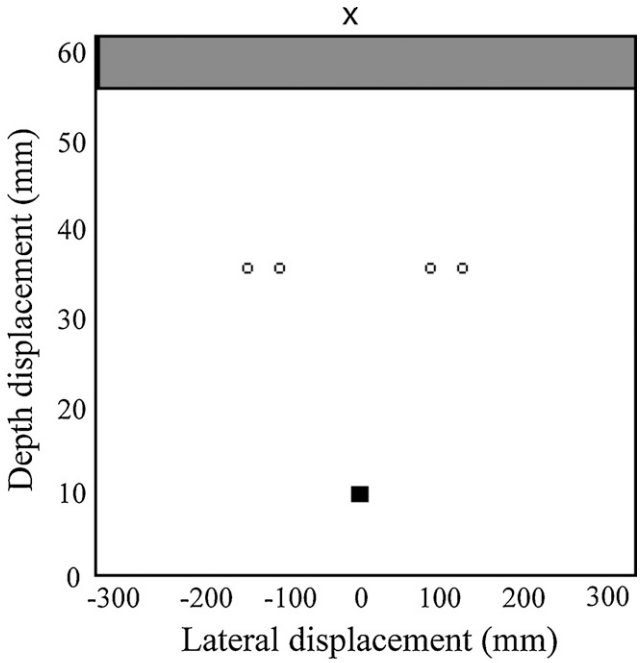

Fig. 3. Experimental set-up for testing obstacle avoidance. The testing board used in Experiments 2 and 3.

Local research ethics committee approval was given for the study.

3.1.2. Experimental equipment

The experimental set-up used in the present experiment has been reported elsewhere (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; Rice et al., 2006; Schindler et al., 2004). Participants faced a 60 cm^2 white board laid horizontally on a table (Fig. 3). The board consisted of a start button located 10 cm from the near edge of the board, a fixation cross located in a central position 16 cm above the surface of the board at its far end, and a 5 cm deep grey target zone, which spanned the far edge of the board. Two grey cylinders (24.5 cm tall and 3.5 cm in diameter) were fixed to the board one on either side of the midline at a distance of 25 cm from the start position and 20 cm in front of the grey target zone. Each of the cylinders could occupy one of two locations, with its inside edge either 8 cm or 12 cm from the midline. The factorial combination of these locations created four possible stimulus configurations. A strip of white card was placed between the two cylinders on

Table 1
Kinematic data for M.H. in the pointing task (Experiment 1)

	Central vision				Peripheral vision			
	Right hand		Left hand		Right hand		Left hand	
	Right field	Left field	Right field	Left field	Right field	Left field	Right field	Left field
RT (ms)	525.33	636.25	507.50	523.75	691.67	592.86	658.75	650.00
MT (ms)	800.40	945.00	816.25	800.00	1065.00	1017.14	923.75	888.75
PVEL (mm/s)	536.49	495.13	464.55	456.68	380.64	423.60	372.43	378.45
%TPV (%)	36.69	36.14	37.17	39.44	36.98	38.96	33.69	36.78

RT: reaction time; MT: movement time; PVEL: peak velocity; %TPV: percentage time to peak velocity.

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every trial to prevent participants using the empty holes to guide them.

Liquid crystal shutter glasses (*Plato System*, Translucent Technologies, Toronto, Canada) were used in order to restrict viewing time of the array. Hand movements of patient M.H. were recorded using a *ProReflex* System, sampling the position of a marker attached to the nail of the right index finger at a sampling frequency of 200 Hz. For control participants, hand movements were recorded using an *Optotrak* system (Northern Digital Inc., Waterloo, Canada); responses were recorded by sampling the position of a marker attached to the nail of the right index finger, at a sampling frequency of 100 Hz. All movements were recorded in full (i.e. from the initial start position to movement offset). Both start position and end position were defined as those recorded on the frame at which hand velocity passed a threshold of 50 mm/s.

3.1.3. Procedure

Participants were required to perform the task with both hands, all participants using their right hand first, followed by their left hand. Participants were instructed to place their right or left index finger on the start button when they were ready to begin each trial. The shutter glasses then opened for 2 s during which time participants were instructed to fixate on the central cross, located at the back of the stimulus board, 16 cm above the surface. While the shutter glasses were open the experimenter visually monitored subjects' eye position to ensure that fixation was maintained. Participants were asked to make their response immediately on hearing a tone, which occurred as the shutter glasses closed. They were asked to reach out and touch the target zone located beyond the two cylinders as quickly as possible. Participants were informed that when a cylinder was present there would always be one on the left and one on the right, and were requested to pass their hand between the two cylinders rather than around the outside edge of the board. Each participant made 60 reaches in a fixed pseudorandom order, with 12 trials for each of the four cylinder configurations and 12 in which no cylinders were present (these latter trials were not included in the main analysis).

3.1.4. Analysis

The main analyses were performed on the weighting indices (dP_L and dP_R) for the left and right cylinder, respectively (McIntosh, McClements, Dijkerman et al., 2004). These indices measure the mean change in lateral position (P) of a participant's index finger (as it crossed an imaginary line joining the two cylinders) that is associated with a shift of one cylinder between its two locations. Thus each weighting index measures how much the participant's movement shifts in relation to a 40 mm shift of one or the other cylinder. If we denote the four different cylinder locations as a = left outer, b = left inner, c = right inner, and d = right outer, we can refer to the four possible stimulus configurations as: ac, ad, bc, and bd. The weighting indices are then given by the following equations:

$$dP_L = \text{mean } P(bc,\ bd) - \text{mean } P(ac,\ ad)$$

[reflecting changes caused by $a \leftrightarrow b$ shifts]

$$dP_R = \text{mean } P(bd,\ ad) - \text{mean } P(bc,\ ac)$$

[reflecting changes caused by $c \leftrightarrow d$ shifts].

A positive value of these weighting indices dP_L and dP_R indicates a shift in movement in the appropriate direction, whereas a zero value would indicate a failure to shift the movement at all in response to a change in cylinder location.

In a second set of analyses, the variability of reaches was assessed, by calculating the variance of P, for each of the four test configurations, and averaging these to give a mean variability score for each participant. Finally, each subject's kinematics were analysed by computing reaction time (ms), movement time (ms), peak velocity (mm/s), and percentage time to peak velocity. These parameters were all computed in the same way as in Experiment 1.

The modified t-test recommended by Crawford and Garthwaite (2002) was used to make statistical comparisons between M.H. and the control group for each dependent variable.

3.2. Results

Fig. 4 depicts the weightings attached to the left and right cylinder in the immediate reaching task with both the left and the right hand for M.H. and controls. Modified t-tests conducted on these data revealed that for left hand reaching there was no significant difference between M.H. and controls for either dP_L ($t = 1.11$, $p = 0.151$) or dP_R ($t = 0.43$, $p = 0.342$). For right hand reaching, there was again no significant difference for dP_L ($t = -0.93$, $p = 0.192$), but there was now a significantly lower value for dP_R in M.H. than in controls ($t = 2.95$, $p = 0.011$). Difference scores between left and right weighting coefficients ($dP_R - dP_L$) were also computed for each subject. This asymmetry score did not differ significantly between M.H. and the controls during left hand reaching ($t = 5.14$, $p = 0.246$), but was significantly greater in M.H. with use of the right hand ($t = -3.07$, $p = 0.009$).

Analysis of the variability of each participant's trajectory showed that M.H.'s variability tended to be higher than the controls for both left hand (M.H. = 130.69; mean con-

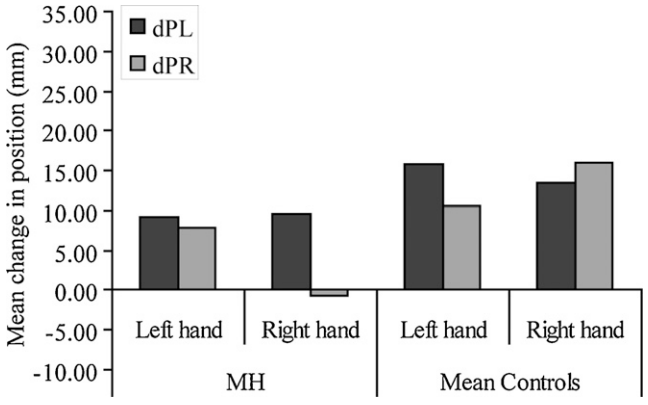

Fig. 4. Immediate obstacle avoidance (Experiment 2). The weightings attached to shifts in the left and right cylinder in the immediate reaching task, for reaches executed by the left or right hand. The left side shows the results for M.H. and the right side the mean results for the controls ($n = 8$). The right cylinder exerted no measurable influence on behaviour when M.H. reached with his right hand.

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Table 2
Kinematic data for M.H. and control participants in the immediate obstacle avoidance task (Experiment 2)

	M.H.		Mean controls	
	Right hand	Left hand	Right hand	Left hand
RT (ms)	591.4	562.5	338.7	285.6
MT (ms)	789.6	826.9	592.6	627.1
PVEL (mm/s)	1321.8	1300.7	1685.7	1555.6
%TPV (%)	39.8	40.4	36.27	37.34

Abbreviations as for Table 1.

trols = 96.72) and right hand reaching (M.H. = 283.81; mean controls = 112.30). This difference, however, reached significance only for the right hand ($t = 2.22$, $p = 0.031$), not the left ($t = 0.944$, $p = 0.188$).

Table 2 illustrates the kinematic data for M.H. and the controls. Modified *t*-tests revealed significantly longer reaction times in M.H. than in controls, for both right hand ($t = 4.42$, $p = 0.002$) and left hand ($t = 4.92$, $p = 0.001$) responding. No other comparison revealed a significant difference between M.H. and controls ($p > 0.12$ for all comparisons).

3.3. Summary

The data from Experiment 2 reveal that M.H. shows a selective deficit in taking account of an obstacle only when located in his right visual field, and only when reaching with his right hand. This result agrees with previous data reported for bilateral optic ataxic patients (Schindler et al., 2004), and is strikingly consistent with M.H.'s pattern of pointing deficit as discovered in Experiment 1. Given that M.H. showed intact obstacle avoidance behaviour in the other three hand/obstacle combinations, the deficits observed clearly cannot be attributed simply to either poor right hand motor control and/or to impaired visual coding of stimulus locations in his right visual field. In Experiment 3 we examined his performance under delayed response conditions.

4. Experiment 3: delayed obstacle avoidance

4.1. Method

M.H., and the control participants who took part in Experiment 2, all participated in Experiment 3. The same experimental set-up and procedure used in Experiment 2 was used again, except that the tone indicating that participants should initiate their response occurred 5 s after the shutter glasses closed. Similar statistical analyses were performed as in Experiment 2.

4.2. Results

Fig. 5 illustrates the weightings attached to the left and right cylinder in the delayed reaching task for both the left and right hand, for M.H. and controls. Modified *t*-tests on these data revealed, as before, no significant difference between M.H. and controls for the left hand for dP_L ($t = 0.83$, $p = 0.217$) or dP_R ($t = 0.25$, $p = 0.404$). In addition, for the right hand too there was

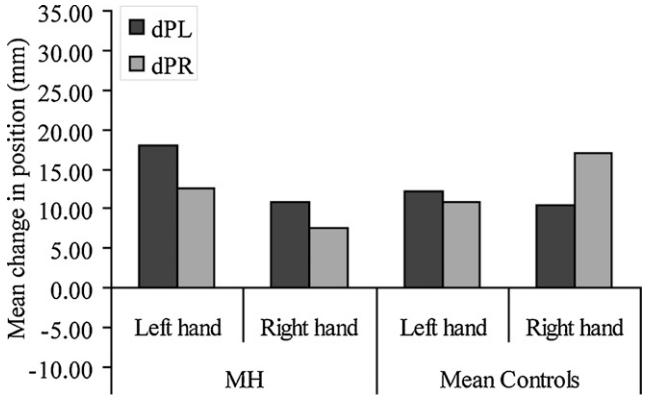

Fig. 5. Delayed obstacle avoidance (Experiment 3). The weightings attached to shifts in the left and right cylinder in the delayed reaching task, for reaches executed by the left or right hand. A clear recovery from the selective obstacle avoidance deficit observed in Experiment 2 is apparent.

now no significant difference between M.H. and controls for either dP_L ($t = 0.042$, $p = 0.484$) or dP_R ($t = 1.142$, $p = 0.145$). This analysis is borne out by computing difference scores ($dP_R - dP_L$) for all subjects. This does not differ significantly between M.H. and the controls during either left hand reaching ($t = -0.65$, $p = 0.268$) or right hand reaching ($t = -0.721$, $p = 0.247$).

The variability of M.H.'s trajectory now tended to be lower than controls, for both the left hand (M.H. = 98.11; mean controls = 155.93) and the right hand (M.H. = 75.50; mean controls = 180.96). These differences, however, did not reach significance for either the right hand ($t = 1.24$, $p = 0.127$), or the left ($t = 0.76$, $p = 0.236$).

Table 3 presents the kinematic data for M.H. and controls. Modified *t*-tests revealed significantly slower reaction time in M.H. than controls for the left hand ($t = 4.17$, $p = 0.002$), but not for the right ($t = 1.14$, $p = 0.147$). There were no other significant differences between M.H. and controls ($p > 0.056$ for all comparisons).

4.3. Summary

These data show that the deficit in right-visual-field obstacle avoidance when M.H. uses his right hand disappears when a delay is required before reaching. Specifically, the qualitative difference between dP_L and dP_R seen during right hand reaching in the immediate task (Experiment 2) disappeared under delayed conditions (Experiment 3). This finding is consistent

Table 3
Kinematic data for M.H. and control participants in the delayed obstacle avoidance task (Experiment 3)

	M.H.		Mean controls	
	Right hand	Left hand	Right hand	Left hand
RT (ms)	447.4	531.9	358.7	300.9
MT (ms)	844.5	859.5	554.3	598.0
PVEL (mm/s)	1104.5	1035.7	1693.8	1502.3
%TPV (%)	37.0	39.3	36.0	34.1

Abbreviations as for Tables 1 and 2.

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with previous studies demonstrating an improvement in visuomotor control following a delay in optic ataxic patients (Milner, Paulignan et al., 1999; Milner et al., 2001), and extends those findings to include behavioural adjustments made to non-target objects.

5. Discussion

The aim of the present study was to examine the hand and field deficits of a patient with optic ataxia caused by a unilateral parietal lesion (M.H.), when he was required to carry out a target-directed pointing task and a non-target-directed obstacle avoidance task. In addition we tested whether a 5 s delay would improve obstacle avoidance behaviour, on the basis of previous evidence that a delay can enable a damaged dorsal stream to be bypassed through ventral stream involvement (Milner, Paulignan et al., 1999; Milner et al., 2001). The results revealed, first, that M.H. has deficits in target-directed pointing especially when using his right hand, and for targets in his right visual field. Second, that M.H. failed to allow for the varying location of a potential obstacle in his right visual field when using his right hand. And finally, that when a 5 s delay was required before response, this obstacle avoidance deficit disappeared.

These results are consistent with previous data in arguing that the visual computations involved in obstacle avoidance behaviour are a function of the dorsal stream, based on complementary outcomes for patients with bilateral optic ataxia (Schindler et al., 2004) and visual form agnosia (Rice et al., 2006). The results go beyond those earlier findings in an unexpected way by demonstrating a highly specific lateralized obstacle-processing deficit in patient M.H. This discovery provides a strong argument that the deficit following bilateral optic ataxia is not due to an overall attentional depletion, or simultanagnosia, as is seen in patients with the full Bálint syndrome. This reasoning is further confirmed by the improvement in reaching seen under delayed response conditions in Experiment 3.

The unusually selective pattern of pointing deficit in M.H., in which the right hand is particularly impaired for right visual-field targets, is matched by an equally selective obstacle avoidance deficit, restricted likewise to right hand reaching, and to potential obstacles only in the right visual field. This suggests that the same areas in the dorsal stream that code target position for guiding goal-directed responses (Connolly, Andersen, & Goodale, 2003; Karnath & Perenin, 2005; Prado et al., 2005) may similarly code the locations of potential obstacles for the purpose of computing suitable reach trajectories for the avoidance of collision.

M.H.'s pattern of deficits is not typical of optic ataxic patients with left parietal lesions, in whom there is generally both a "visual field effect" and a "hand effect", but not a hand by visual field interaction. This results in their making inaccurate reaches with all hand/field combinations except for the left hand/left visual field (Perenin & Vighetto, 1988). While M.H. does show both a clear field and hand effect in the target directed reaching task (Experiment 1), with his errors being highest with his right hand and in his right visual field, Fig. 2 shows clearly that these statistical main effects were mainly driven by very large errors when using his right hand in his right visual field, as also reflected in the three-way interaction between visual field, viewing condition and hand. This pattern matches our finding in the immediate obstacle avoidance task, in which M.H. only differed significantly from controls when using his right hand with respect to obstacles in his right visual field. Although unusual, however, M.H. is not unique in showing this pattern of deficit restricted to the right hand and right field following left parietal damage (e.g. Rondot, De Recondo, & Ribadeau Dumas, 1977; Tzavaras & Masure, 1976).

While optic ataxia is traditionally defined as a disorder of accuracy when reaching towards visual targets (Bálint, 1909), our understanding of the disorder has evolved considerably since then. For example, it has been shown that optic ataxia patients have deficits orienting and shaping the hand correctly (Goodale, Meenan et al., 1994; Jakobson et al., 1991; Jeannerod, 1986; Perenin & Vighetto, 1988), and in both the programming (Ishihara et al., 2004; Milner et al., 2003) and the on-line control (Gréa et al., 2002; Pisella et al., 2000) of target-directed movements. Because of these advances in knowledge of optic ataxia, it has been proposed that the disorder should be re-defined as a more general difficulty in the real-time visuomotor guidance of action (Milner & Goodale, 1995). Schindler et al. (2004) tested the extent of such a proposed generality by asking whether the visuomotor deficits include not only the processing of action targets, but also the processing of non-targets, and their results strongly supported such an extended description. A notable commonality shared by all of these various visuomotor deficits in optic ataxia is a relative failure to use extrafoveal visual information effectively for immediate action guidance (Pisella et al., 2000). The results of the present study provide further support for this generalized conception of optic ataxia.

The results of imposing a delay in the present study further confirm previous work showing that such a delay tends to improve visuomotor deficits in optic ataxic patients (Himmelbach & Karnath, 2005; Milner, Dijkerman et al., 1999; Milner et al., 2001; Revol et al., 2003). We have extended previous findings by demonstrating a similar effect in the processing of non-target stimuli during reaching. Our results thus broaden the applicability of Milner and Goodale's (1995) proposals regarding the temporal operating characteristics of the dorsal and ventral streams to include a further domain of visuomotor processing. The argument would be that although obstacle avoidance is normally mediated by the dorsal stream, and is therefore selectively impaired in patient M.H., under delayed conditions the task becomes ventral stream mediated, allowing a recovery in the impaired hand/field to a level within the normal range. An implication of this argument, of course, is that the patient's ventral stream gives him a complete subjective view of the array which 5 s later can be translated into appropriate motor control. Yet paradoxically, this intact percept does not *at the time* provide the means to allow him to make appropriate motor adjustments for immediate right hand reaching.

Given the selective nature of M.H.'s immediate pointing and obstacle avoidance deficits, it is clear that neither result can be attributed to a motor problem with his right hand or to a sensory deficit in his right visual field. This argument is further

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strengthened by his intact performance under delay conditions. We propose that when acting immediately (on dorsal stream information), M.H.'s reaches are less consistently programmed, whereas when acting after a delay he is using visual (and motor) systems that are almost as effective as those of healthy controls. Of course M.H., unsurprisingly given his extensive brain damage, tended to show longer reaction times than controls throughout the study. It is notable, however, that this slowing was present when using both the right and the left hand in the immediate reaching task, so it can provide no insight into the selective nature of M.H.'s deficit in that task.

An interesting question that arises from our results is whether the visuomotor mechanisms of M.H.'s left dorsal stream are processing right visual-field stimuli at all when he is using his right hand. Clearly the system does not process such stimuli sufficiently for full functional visuomotor control to be achieved, whether in pointing (Experiment 1) or obstacle avoidance (Experiment 2). But does the system at least *detect* the stimulus, while unable to localize it for visuomotor purposes? The answer as regards Experiment 1 is clear. Although M.H. made sizeable spatial errors to targets in his right visual field when using his right hand (his average error for targets located at 20 and 25 cm from the midline was 7.6 cm: see Fig. 2), he nonetheless responded differentially with respect to the different target locations. Previous studies of optic ataxia point to the same conclusion. That is, although the human dorsal stream is damaged in optic ataxia, it retains an ability to process the presence of targets, despite not processing their location effectively for action.

A similar inference, though less obvious, can be made for obstacle avoidance in real time (Experiment 2). Here the zero weighting that M.H. attaches to the rightward cylinder (dP_R) when using his right hand shows that he fails to adjust his responses to the varying locations of the object. But if he was failing to detect the object on the right completely (i.e. if he was only detecting the left object), he should have tended to veer towards the right when reaching with his right hand, perhaps sometimes colliding with the undetected object. Previous research using a reaching paradigm similar to the present one showed that on interspersed trials when only one obstacle really was present on the left or right, healthy subjects shifted their movements by several centimetres relative to when both obstacles were present (McIntosh, McClements, Schindler et al., 2004). In the present study, in contrast, M.H.'s reaches never veered more than 4.5 cm from the midline when he used his right hand (as compared with a maximum deviation of 4.2 cm when he was using his left hand); and he never collided with the rightward obstacle. Indeed M.H.'s right hand trajectories actually veer less far rightwards than those of controls, whose maximum deviation from the midline averaged 5.2 cm. Thus his visuomotor difficulty seems not to be a failure to register the rightward object, but rather a specific failure to take account of its varying location as a potential obstacle. In summary, we suggest that both the pointing and obstacle avoidance deficits observed in M.H. can be attributed to a specific failure to use the location of the target (Experiment 1) or non-target (Experiment 2) to guide action.

In conclusion, the results of the present experiments show that obstacle avoidance behaviour in an optic ataxic patient shows a pattern of visuomotor impairment closely related to his accuracy in a visual pointing task. This deficit shows recovery, however, when a 5 s delay is required before response. These results can be taken as confirmatory evidence that automatic obstacle avoidance is a function of the dorsal stream of visual processing (McIntosh, McClements, Dijkerman et al., 2004; Schindler et al., 2004; Rice et al., 2006). Our results also add support to the idea that when reaching is delayed, a quite different visuospatial coding system, intact in our patient, comes into play to guide reaching behaviour—a system that may depend on the ventral stream of processing.

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