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RESEARCH ARTICLE

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Intact automatic avoidance of obstacles in patients with visual form agnosia

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Abstract In everyday life our reaching behaviour has to be guided not only by the location and properties of the target object, but also by the presence of potential obstacles in the workspace. Recent evidence from neglect and optic ataxia patients has suggested that this automatic obstacle avoidance is mediated by the dorsal, rather than the ventral, stream of visual processing. We tested this idea in two studies involving patients with visual form agnosia resulting from bilateral ventral-stream damage. In the first study, we asked patient DF to reach out and pick up a target object in the presence of obstacles placed at varying distances to the left or right of the target. We found that both DF and controls shifted their trajectories away from the potential obstacles and adjusted their grip aperture in such a way as to minimize risk of collision. In a second study, we asked DF and a second patient, SB, to either reach between, or to bisect the space between, two cylinders presented at varying locations. We found that both patients adjusted their reach trajectories to account for shifts in cylinder location in the reaching task, despite showing significantly worse performance than control subjects when asked to make a bisection judgement. Taken together, these data indicate that automatic obstacle avoidance behaviour is spared in our patients with visual form agnosia. We attribute their ability to the functional intactness of the dorsal stream of visual processing, and argue that the ventral stream plays no important role in automatic obstacle avoidance.

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Introduction

In everyday life we automatically tailor our movements so as to prevent collisions with potential obstacles in our workspace. In the laboratory similar behaviours have been observed. For example, Jackson et al. (1995) found that the placement of non-target objects in the workspace caused changes in both the transport and grasp components of a reach, especially when performed in visual open loop conditions (i.e. when visual feedback is denied). In other studies, it was reported that even a non-target LED would cause reaching movements to veer away from the LED (Howard and Tipper 1997; Tipper et al. 1997). Although the authors conceptualized this effect as a kind of attentional repulsion, in functional terms it may reflect a failsafe mechanism to maintain sight of potential obstacles in order to minimize the likelihood of colliding with them. This failsafe mechanism may be automatically recruited even when there is no actual physical risk of collision. Tresilian (1998) presented data in support of this interpretation, arguing that both the grasp and transport components of prehension movements are adjusted to avoid potential obstacles. Tresilian proposed

that people move so as to avoid the hand coming within a minimum preferred distance from non-target objects within the workspace.

More recently, Mon-Williams and McIntosh (2000) have shown that as the distance between two flanking obstacles gets smaller, movement time to grasp a target object increases, according to a quasi-Fitts' Law function (Fitts 1954). In a further investigation, Mon-Williams et al. (2001) found that the presence of obstacles during a reach to grasp task caused both increases in movement time and decreases in maximum grip aperture, but in varying proportions depending on the layout of the workspace. They suggested that their findings indicate a flexible control strategy in which movements are adjusted to avoid collision with obstacles in a subtle and precise manner.

Until very recently, there have been no investigations directed at understanding the neural underpinnings of these various aspects of non-target processing in goal directed reaching. In contrast, a host of neurobehavioural and neurophysiological studies are in agreement that the visual control of target-directed reaching and grasping depends upon systems in the dorsal stream of cortical processing (Milner and Goodale 1995; Jeannerod 1997; Goodale and Milner 2004). Nevertheless, non-target processing clearly plays an important role in determining the parameters of reaching and grasping movements. One of the first studies of non-target processing following brain damage was performed by McIntosh et al. (2004a). They tested 12 neglect patients and 12 healthy control subjects on a bisection task and a reaching task, in both cases using the same spatial layout. Subjects were presented with two cylinders, one on the left and one on the right, each of which could be located in one of two positions. In the bisection task they were required to judge the midpoint between the two cylinders by making a pointing response, while in the reaching task they were required to touch a wide target zone located beyond the two cylinders, by reaching between them. The former can be regarded as an explicit bisection task, while the latter is an implicit one. The results showed that 10 out of the 12 neglect patients performed similarly to controls on the reaching task, taking full account of both cylinder locations as they carried out the movements. This result contrasted with their behaviour in the bisection task, where the patients took little account of the varying locations of the left cylinder when making their spatial judgements. McIntosh et al. (2004a) argued that this preservation of non-target processing during reaching in most neglect patients might be due to the sparing of dorsal-stream cortex in and around the intraparietal cortex (Culham and Kanwisher 2001). The implication of their argument was that the two patients who did not show such a preservation must have had lesions that included concomitant damage to dorsal stream areas.

These results suggest that the adjustments made to reaching movements with respect to potential obstacles are not subject to the same neglect of leftward objects to which conscious bisection judgements are prone. They do not, of course, show that the patients were taking the left cylinder into account without being visually aware of it. The patients were free to move their eyes and no attempt was made to discover what they saw or did not see. Therefore in a separate study (McIntosh et al. 2004b), a patient with visual extinction was tested in a comparable reaching task. Instead of 2 cm wide cylinders, thin poles were used, and they were visible only briefly: by this means it was possible to induce extinction of the left pole on about half of the test trials. On different trials, either the left pole alone, the right pole alone, both, or neither of the poles was present. The results showed that the patient took significantly different reaching routes according to whether the left, right, or both poles were present, much as healthy control subjects did. Moreover, his reach trajectories when both poles were present were identical on trials where he reported seeing the left pole and on those when he reported not seeing it.

Taken together, the results of these two studies are consistent with the hypothesis that obstacle avoidance is subserved by the same superior parietal networks as the target-directed aspects of reaching, and that this processing does not require conscious awareness of the potential obstacles (Milner and McIntosh 2004). More direct evidence for this hypothesis was obtained in a third study in which two patients with optic ataxia, resulting from bilateral lesions of the dorsal stream, were tested on essentially the same two tasks used by McIntosh et al. (2004a). In this study (Schindler et al. 2004), the optic ataxic patients failed completely to shift their trajectories with respect to any changes in cylinder location in the reaching task, while taking full account of shifts of both cylinders when required to bisect the space between them. These patients thus exhibited the opposite pattern to that typically seen in neglect patients.

The results of these studies fit well within the framework of our current functional understanding of the ventral and dorsal processing streams (Milner and Goodale 1995; Goodale and Milner 2004). That is, like target-directed reaching and grasping movements, it can be proposed that automatic obstacle avoidance is a dorsal stream function (abolished when superior parietal cortex is damaged, as in optic ataxia, but typically preserved in neglect, where the damage is predominantly temporo-parietal). Bisection, on the other hand, depends on a conscious strategy which optic ataxic patients can implement using perceptual information processed within their ventral stream and its right temporo-parietal elaboration; both of which may remain largely intact. A prediction from this interpretation is that while damage to the ventral stream itself might be expected to impair gap bisection to some degree (assuming that it provides an important input route to the temporo-parietal region damaged in neglect), it should entirely spare obstacle avoidance.

In contrast to optic ataxia, visual form agnosia is associated with damage to the ventral stream of

processing. Benson and Greenberg (1969) first introduced the term visual form agnosia when describing a patient (Mr S) whose recognition deficits they believed could be attributed to a primary defect in form discrimination. They suggested that the disorder was associated with an intact ability to deal with the simple features of an object, but a specific inability to put such features together to permit form discrimination and perception. This loss resulted in the patient having a severe inability to recognize everyday objects, and particularly drawings of objects, by virtue of their shape (see review by Heider 2000). In the present paper, we have tested a patient with a very similar pattern of visual impairment to Mr S (DF: Milner et al. 1991), who has been extensively studied (see Milner 1997; Goodale and Milner 2004). Recently, James et al. (2003) have shown that DF has bilateral posterior cortical damage remarkably coincident with the lateral occipital (LO) area (Malach et al. 1995; Kanwisher et al. 1997). Indeed, when functional MRI (fMRI) was used to examine her brain activation in response to complete versus fragmented line drawings of objects, the subtraction of which defines area LO in healthy subjects, no net activation was found (James et al. 2003). It was inferred from these results that it was DF's bilateral damage to area LO that was the direct cause of her visual form agnosia, and by extension that similar damage is the cause of this impairment in other patients as well. In contrast, DF, as demonstrated in a number of studies (Goodale et al. 1991; Milner et al. 1991), has rather well-preserved visuomotor control in simple reaching and grasping tasks, which has been attributed to a functionally intact dorsal stream of visual processing (Milner and Goodale 1995; Milner 1997). This conjecture has now been confirmed using fMRI (James et al. 2003; Culham 2004).

The aim of the present experiments was to examine obstacle avoidance behaviour in visual form agnosia in order to assess the relative contributions of the dorsal and ventral streams to automatic obstacle avoidance. We define obstacle avoidance as behaviour in which a participant moves a body part over, away from or around non-targets, in order to avoid potential collision. [Nonetheless, empirical evidence suggests that the brain mechanisms controlling such behaviour may also sometimes treat stimuli that present no real risk of collision (e.g. LEDs) in a qualitatively similar way (Tresilian 1999)]. Such behaviour should be inversely related to the distance between target and obstacle (i.e. the closer the obstacle to the target, the greater the effect on performance). In the first experiment DF was asked to reach out and grasp an object in the presence of a secondary object, placed either to the left or the right of the target, at varying distances. In the second experiment DF and a second visual form agnosic patient, SB, were asked to either reach between or bisect the space between two cylinders in a manner similar to the previous studies of McIntosh et al. (2004a) and Schindler et al. (2004). If automatic obstacle avoidance is subserved by the dorsal stream of processing alone, it would be predicted that in the first experiment, DF would take full account of the obstacle locations relative to the target, by systematically shifting her reach trajectories and modifying her grip aperture, in the same manner as controls. In the second experiment it was predicted that although both patients might show somewhat impaired performance on the bisection task due to their damaged ventral streams, they should perform in a similar way to controls when required to reach between the two cylinders, given their functionally intact dorsal streams. In other words, a partial double dissociation between optic ataxic and visual form agnosic patients was predicted on these respective perceptual and visuomotor tasks.

Experiment 1

Method

Participants

Patient DF and six controls took part in the study: three females (average 27.3-year old, SD 4.6 years) and three males (average 25.7-year old, SD 2.1 years)[1]. All participants were right-handed by self-report, had normal or corrected to normal vision, and no history of neurological disorders.

DF was 43 years old at the time of testing, and had developed visual form agnosia as a result of carbon monoxide poisoning 9 years earlier. She was extensively tested by Milner et al. (1991), her deficits including a failure to recognize objects visually, and difficulties in discriminating shape, lightness (see also Milner and Heywood 1989), orientation, symmetry and texture differences. She was also unable to copy drawings or letters, had impoverished reading abilities, and experienced difficulty estimating the speed of objects. Despite these deficits she had preserved visual acuity, colour vision, tactile recognition and verbal intelligence. She could partially describe objects, particularly their surface properties, and could then make reasonable guesses as to what they were. Though finding it difficult to describe her visual experience, she said that objects appeared "blurred" and tended "to run into each other". EEG showed bilateral abnormalities, most prominent posteriorly and in temporal regions. Early MRI scans showed abnormalities in occipital cortex bilaterally, with the damage extending laterally in the ventral part of the occipital lobe (area 18) and dorsally in the posterior occipitoparietal region, her primary visual cortex remaining intact (Milner et al. 1991). A recent study (James et al. 2003) has shown that DF's principal lesions correspond bilaterally with the location of the LO area

[1]In Experiment 2 two groups of control participants were tested; one group age-matched to D.F. and one group age-matched to S.B. A comparison between the results of the two control groups revealed no difference, suggesting that the age difference between them did not affect performance.

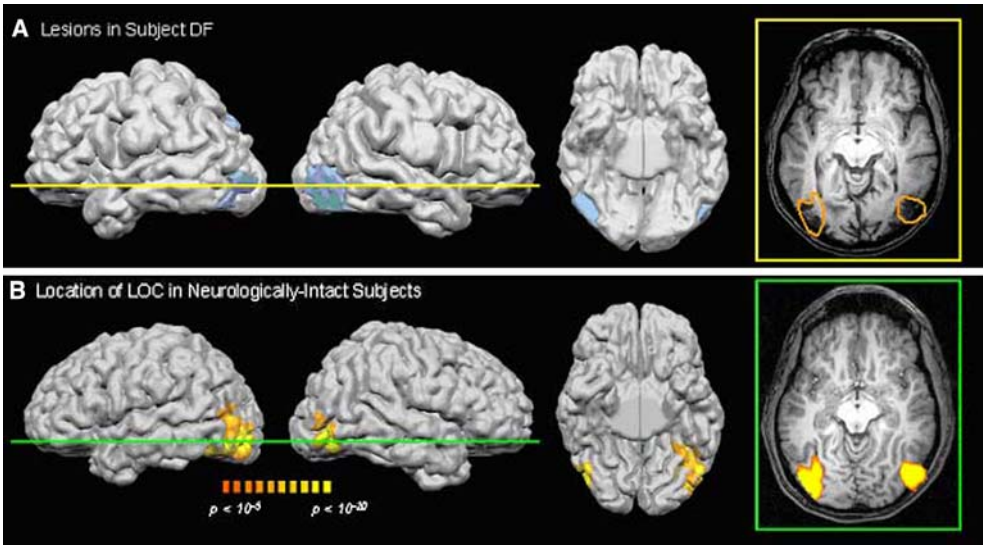

Fig. 1 Ventral stream lesions in patient DF shown in comparison with the expected location of the LO complex in healthy subjects, taken from MRI scan data. *A* DF's brain has been rendered at the pial surface (outer grey matter boundary). Lesions were traced on slices that indicated tissue damage, and rendered on the pial surface in *pale blue*. Lateral views of the left and right hemispheres are shown, as is a ventral view of the underside of the brain. The rightmost image shows a slice through the lesions ($z = \pm 8$). *B* The expected location of LOC based on group data from seven neurologically intact participants is shown on one individual's pial surface and on a slice through the $z = \pm 8$ plane. The activation in the slice is outlined in orange in panel *A* for comparison with the lesions in DF's brain. (Reproduced with permission from James et al. 2003)

in the ventral stream in healthy subjects (see Fig. 1), along with damage to the left posterior parietal cortex.

Apparatus

The equipment used in the present experiment is depicted in Fig. 2. Participants placed their index finger and thumb on a start position located directly in front of them. They were presented with a green target object, which was located 25 cm away from the start point, and aligned with their body midline. There were six possible obstacle locations, either 3, 6 or 9 cm away from the inside edge of the target. Both target and obstacle were 3 cm wide, 2 cm deep, 5 cm high. The target was green in colour, while the obstacle was always black. Hand movements were recorded using *Minibird* (Ascension Technology Ltd, VT, USA), which sampled the positions of two markers attached to the index finger and thumb at a frequency of 86.1 Hz. Movements were recorded in full (i.e. from initial start position to end of each movement). Recordings were filtered at 10 Hz, and the start and end of each movement were defined by a 5 cm/s threshold, maintained for ten frames at the start.

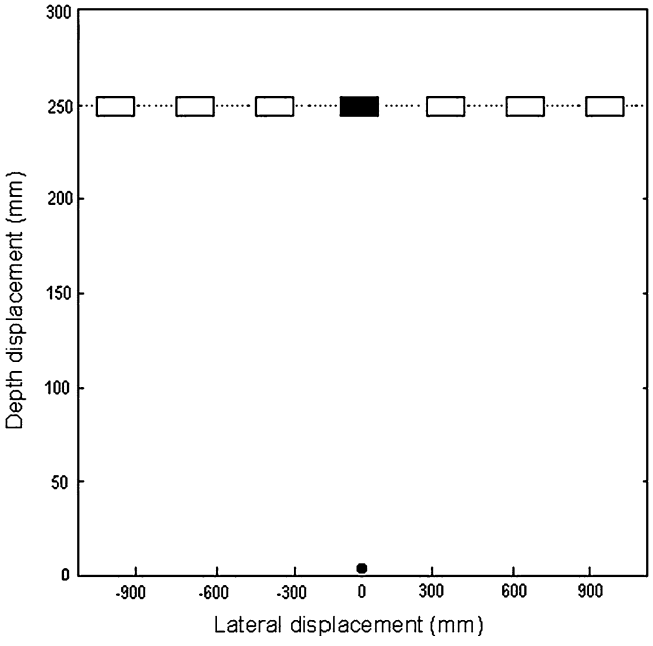

Fig. 2 The experimental arrangement used in Experiment 1. The start position is shown as a *filled black circle*, the target as a *filled rectangle*, and the six possible obstacle locations as *empty rectangles*

Procedure

The experiment consisted of a simple grasping task performed in free vision. Subjects were asked to reach out and grasp the target object as quickly as possible using the right hand. There were seven different conditions. In one, the target was presented alone, while in each of the other six conditions, the obstacle was present alongside the target object. On each trial, the subject was cued to respond by a verbal "go" signal given by the experimenter. Each subject performed a block of 56 trials, with eight trials per condition presented in a fixed pseudo-random order. The data were processed using custom written Labview programs (National Instruments Inc., Austin, TX, USA).

Results

Analysis

The average x–y trajectory of the index finder and thumb was computed for each condition in which there was an obstacle present for both DF and controls. The x trajectory refers to the left/right dimension with respect to the observer, and the y trajectory refers to the forward/backward dimension. These trajectories were normalized to the start position (which varied slightly from trial to trial) and then modified t-tests, recommended by Crawford and Garthwaite (2002) were used to compare DF to the controls at 1-cm intervals throughout the movement in each of the conditions.

In addition, the following kinematic variables were computed and used for analysis: maximum grip aperture, movement time, peak velocity, time to maximum grip aperture, time to peak velocity, percentage time to maximum grip aperture (expressed as a percentage of total movement time) and percentage time to peak velocity (expressed as a percentage of total movement). Maximum grip aperture was defined as the maximum 3-dimensional separation of the markers attached to the index finger and the thumb. Movement time was defined as end time (defined as the time at which the velocity of the marker attached to the thumb fell below 50 mm/s) minus start time (defined as the time at which the velocity of the marker attached to the thumb exceeded 50 mm/s for at least 100 ms). Peak velocity was defined as the maximum velocity of the marker attached to the thumb. Time to peak velocity was the time at which peak velocity occurred minus the start time. Percentage time to maximum grip aperture was time to maximum grip aperture expressed as a percentage of total movement time. Percentage time to peak velocity was the time to peak velocity expressed as a percentage of total movement time. For each of these seven variables an individual ANOVA was carried out for DF and each of the control subjects, with two factors (1) Obstacle position (left/right) (2) Obstacle distance (3 cm/6 cm/9 cm) (target-only trials were excluded from the analysis).

Trajectory

Figure 3 shows the average trajectory of the index finger and thumb for each condition for DF and controls, normalized for the start position. These graphs clearly show that both DF and the controls shift their trajectory to the right in the presence of a left obstacle, and shift their trajectory to the left in the presence of a right obstacle, the largest shift occurring when the obstacle is close to the target. A modified t-test was conducted comparing the trajectory for DF and controls every 1 cm of the movement; this revealed no significant differences between DF and the controls.

Kinematics

Table 1 shows the kinematic data for DF and the controls in each condition. An individual ANOVA was used to assess the effect of obstacle position (left/right) and obstacle distance (3 cm/6 cm/9 cm) for DF and each of the controls. The results for the control subjects were considered to be consistent if significant effects were observed in four or more of the six controls. For DF a significant effect of obstacle position was observed for peak velocity ($P < 0.05$), in that DF achieved a higher peak velocity when the obstacle was present on the left. No other effects of obstacle position were observed in DF and no consistent effects of obstacle position were observed in the control subjects. A significant effect of obstacle distance on maximum grip aperture was observed for DF ($P < 0.01$), with an increase in maximum grip aperture as distance between the target and obstacle increased. Similar effects and patterns were consistently observed in the control subjects ($P < 0.01$). A significant effect of obstacle distance on movement time was present for DF ($P < 0.05$), in that DF shows an increase in movement time when there is an increase in distance between the target and obstacle. A significant effect of obstacle distance on movement time was also consistently observed in the control subjects ($P < 0.05$), but the pattern of results goes in the opposite direction, with a decrease in movement time as distance between obstacle and target increases. A significant effect of obstacle distance on percentage time to maximum grip aperture was also observed for DF ($P < 0.05$), in that DF showed an earlier time to maximum grip aperture as distance between the target and obstacle increased, while no such pattern was observed consistently for control subjects. Finally a significant effect of obstacle distance on percentage time to peak velocity was observed for DF ($P < 0.001$), reflecting an earlier time to peak velocity for the far obstacle location compared to the other conditions. Such an effect was also consistently observed in control subjects ($P < 0.05$), but this was due to the peak velocity being reached at later times as the distance between target and obstacle increased. No other significant effects of obstacle distance were observed for DF or consistently for control subjects.

Discussion

The aim of Experiment 1 was to assess patient DF's performance (in comparison with controls) when asked to reach out and grasp a target object in the presence of potential obstacles placed at different locations. The results demonstrate that the average trajectory taken by the hand was similar in both DF and controls for each obstacle condition. In other words, DF shifts her overall trajectory to the left in the presence of a rightward obstacle and to the right in the presence of a leftward obstacle, in a manner comparable to healthy subjects.

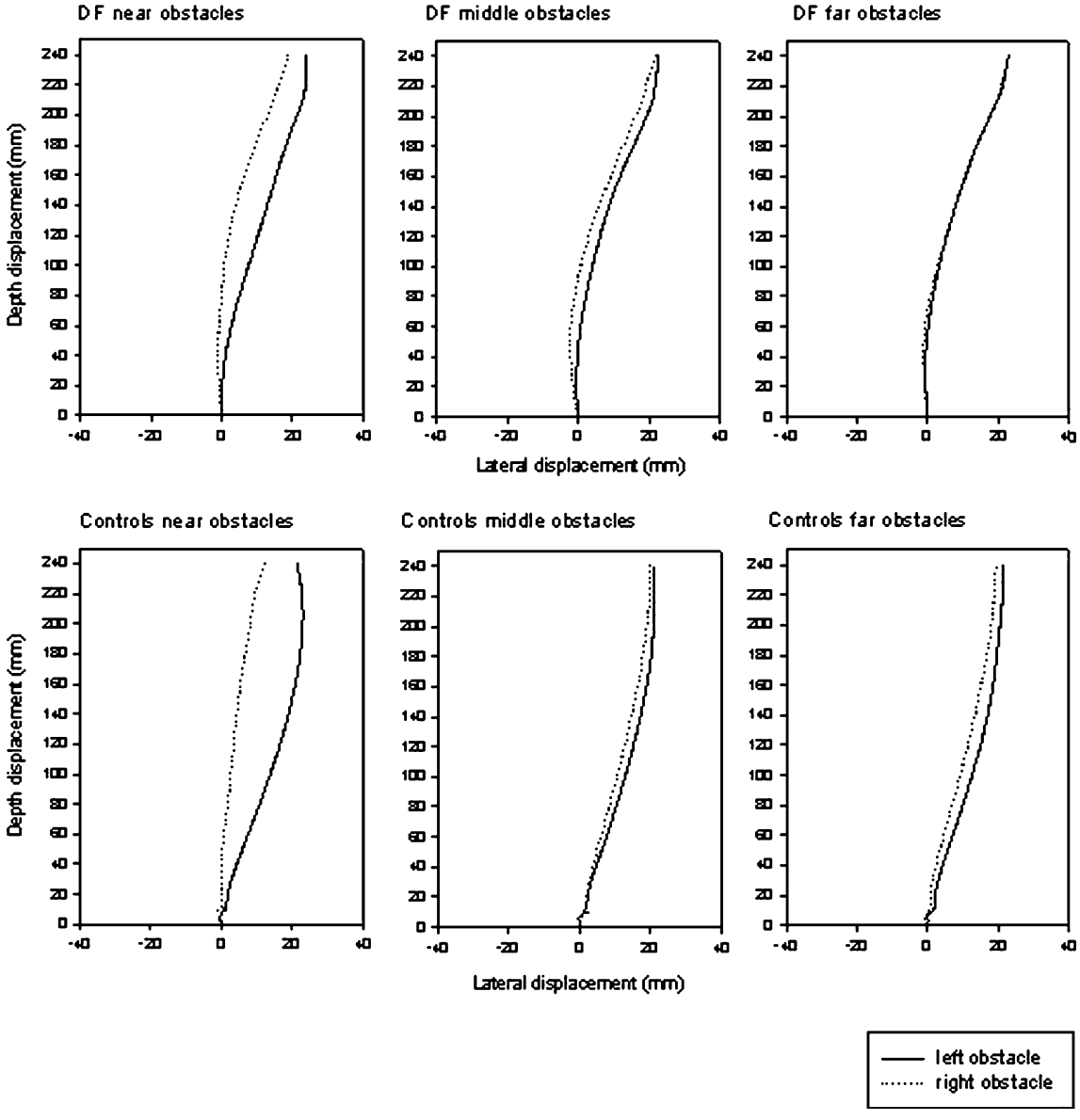

Fig. 3 Experiment 1: Graphs depicting the reach trajectories (normalized for start position) taken by DF (*top* three graphs) and controls (*bottom* three graphs) for each of the three obstacle locations. The *solid line* represents reach trajectories when the obstacle was present on the left and the *broken line* represents reach trajectories when the obstacle was on the right

We suggest that this intact obstacle avoidance behaviour is achieved by virtue of her functioning dorsal stream of visual processing (James et al. 2003).

The kinematic results confirm the observations by Mon-Williams et al. (2001) that the presence of obstacles during a reach-to-grasp task leads to an increase in movement time and a decrease in maximum grip aperture in healthy subjects. They further confirm that these effects are highly dependent on the distance of the obstacle from the target (Mon-Williams and McIntosh 2000), with a decrease in maximum grip aperture and an increase in movement time being seen as the target-obstacle separation decreases. In addition we have found that time to peak velocity (expressed as a percentage of movement time) occurs later as distance between the target and obstacle increases in healthy individuals. All of this suggests that the extent to which subjects adjust the transport and grasp components of the reach in the presence of a potential obstacle is inversely related to the target-obstacle separation, and thereby directly related to the risk of collision with the obstacle. DF's kinematic results similarly showed a decrease in maximum grip aperture as distance between the target and obstacle became smaller, strengthening the finding that she exhibits intact obstacle avoidance behaviour. One surprising difference between DF and the controls, however, is that as the target-obstacle separation increased she showed a slower movement time. In other words, the closer the obstacle was to the target, the faster were DF's reaches. It is possible that this is due to the fact that the

Table 1 Experiment 1: kinematic data for DF and healthy controls for each of the test conditions, including maximum grip aperture (MGA), movement time (MT), peak velocity (PV), time to maximum grip aperture (TMGA), time to peak velocity (TPV), % time to maximum grip aperture (%TMGA), % time to peak velocity (%TPVEL)

		Far left	Middle left	Near left	Target only	Near right	Middle right	Far right
MGA	DF	68.17	67.29	65.32	67.44	64.10	68.83	70.29
	Controls	81.66	80.86	71.56	80.19	70.32	79.29	82.66
MT	DF	1058.54	951.58	949.46	1042.78	956.21	991.03	1027.03
	Controls	524.92	553.83	586.44	517.02	608.20	565.44	525.18
PV	DF	816.66	814.70	823.08	793.60	784.05	792.92	794.56
	Controls	1294.91	1251.43	1269.48	1274.23	1130.20	1211.11	1293.34
TMGA	DF	591.30	591.15	599.74	587.68	539.94	603.89	576.79
	Controls	303.61	317.86	319.89	303.25	319.84	332.90	315.41
TPV	DF	312.18	329.01	321.83	318.26	304.51	334.47	285.53
	Controls	202.81	206.64	198.99	197.76	196.10	222.59	201.30
%TMGA	DF	56.11	62.50	63.79	56.59	57.06	61.49	56.26
	Controls	59.17	57.72	55.60	59.47	52.62	58.66	60.22
%TPVEL	DF	29.62	34.84	34.11	30.54	32.15	34.06	27.95
	Controls	40.89	38.12	34.79	39.31	32.85	39.56	40.09

presence of the non-target obstacles in the workspace enriched DF's spatial representation of the scene, giving her more confidence to move faster. In addition, DF also showed an atypical pattern of results when time to maximum grip aperture and time to peak velocity were expressed as a percentage of movement time. It should be noted, however, that in this study no constraints were placed on the subjects regarding speed of movement, and DF's movement time was approximately twice as long as control subjects in all conditions. This makes comparisons of her kinematic data difficult.

There has been much debate in the literature between the respective merits of 'distractor' accounts and 'obstacle avoidance' accounts of the effects of non-target objects on motor behaviour (Tipper et al. 1997; Castiello 1999). It has been argued that effects such as those observed in the present experiment cannot be explained by obstacle avoidance alone and may be due to the fact that the non-target objects serve as distractors and cause competition for attention (Castiello 1999). For example, studies have shown that non-target objects in the form of an LED (which would cause no risk of collision) can cause reaching movements to veer away. Although the authors interpret their findings as a kind of attentional repulsion (Howard and Tipper 1997; Tipper et al. 1997), Tresilian (1999) argues that this additional postulate is unnecessary for explaining the data. Since participants were instructed to attend to the LED, their behaviour could have been an avoidance response to ensure unrestricted viewing to comply with task instructions. Such an explanation is supported by the observation that participants only veered away from the LED when it was possible for their reaching limb to obscure a clear view of it. If the non-target objects used in the present experiment were treated as distractors rather than obstacles, it is difficult to explain why participants not only moved their hand trajectories consistently away from them, differentially according to the distance of the non-target object from the target, but also opened their grip less widely for the closest non-target objects. Given this pattern of findings, it seems more appropriate to discuss the results of the present experiment within the framework of obstacle avoidance (i.e. that participants move away from the non-target objects in the work space and adjust the kinematics of their movements in order to minimize risk of collision). Of course, this functional interpretation does not exclude the possibility that the actual neural mechanism whereby the trajectories change could involve some kind of inhibitory process between the neuronal correlates of the target and non-target locations, thereby causing a kind of 'repulsion' effect. But then of course a different interpretation would have to be sought for the changes observed in grip size.

In summary, the results of Experiment 1 show that the presence of obstacles in the workspace causes both DF and healthy subjects to adjust their reaching trajectory, and decrease their maximum grip aperture, ostensibly in order to avoid the possibility of collision. The effects observed are dependent on the distance of the non-target object from the target, with those closest to the target having the greatest effect. The data thus confirm our prediction that DF should have intact obstacle avoidance behaviour, and they thereby provide convergent support for the idea that such behaviour is mediated by the dorsal stream of visual processing.

One weakness of the present experiment, however, is that we did not have a control task that would enable us to demonstrate a dissociation between DF's intact visuomotor behaviour and impaired perceptual processing. Such a task (i.e. one that is formally similar to the visuomotor task but which demands an element of perceptual processing) would enable us to make a stronger claim regarding DF's intact obstacle avoidance behaviour. In addition, the present study had no constraints placed on the subjects regarding speed of movement. Finally, although DF is the most extensively studied patient with visual form agnosia, a second patient would enable us to make stronger claims for preserved obstacle avoidance behaviour in patients of this kind.

In Experiment 2, we sought to examine whether we could extend the results of Experiment 1 to demonstrate a partial double dissociation between visual form agnosia and optic ataxia, using tasks similar to those of Schindler et al. (2004). In that study, two patients with bilateral optic ataxia showed a complete failure to heed the changing obstacle locations during a reaching task, while both showed a full appreciation of the same two objects when making a bisection judgement of the space between them. In the present experiment we were able to test both DF and also a second patient with visual form agnosia, SB. The experimental paradigm extends the previous experiment, not only by including a perceptual control task, but also in that subjects are given instructions regarding speed of movement.

Experiment 2

Method

Participants

Two patients with visual form agnosia (DF and SB) and 16 age-matched controls took part in the study. Eight of the controls were females age-matched to DF (average 46.3 years, SD 7.4 years), while the others were males age-matched to SB (average 34.4 years, SD 3.5 years). All participants were right-handed by self-report, had normal or corrected to normal vision and no history of neurological disorders.

DF was 48 years old at the time of testing, while SB was 34 years old. Patient SB had developed visual form agnosia following meningoencephalitis at 3 years old. As shown in the extensive studies of Lê et al. (2002), his deficits include achromatopsia, prosopagnosia, alexia and object agnosia. Like DF, SB typically focuses on parts of objects rather than the objects themselves, and can process local aspects of shapes while failing to link and integrate them as a global whole. SB also shares DF's ability to generate and manipulate visual images. SB performs better than DF in matching meaningful and meaningless objects, as well as in copying drawings (relying on feature by feature analysis of the objects), and in being able to navigate his way confidently in both familiar and non-familiar environments. He also has a striking ability to use motion information to help him identify objects. MRI scans show lesions of the occipitoparietal and occipitotemporal regions in the right hemisphere and the occipitotemporal junction of the left hemisphere. The right hemisphere lesion is reported to include complete or partial damage to areas V2, V3, V4, V5 and LO, and there is limited damage to the right supramarginal gyrus. There is a spared region in the right occipital pole including the calcarine fissure (V1), in its rostral and superior aspects. In the left hemisphere, the lesion involves mainly the ventrolateral visual cortex, including the fusiform gyrus and area LO (Lê et al. 2002) (see Fig. 4).

The study was carried out according to the principles of the Declaration of Helsinki, on the basis of informed consent, and was approved by the local research ethics committee.

Apparatus

The experimental set-up is depicted in Fig. 5. Participants faced a 60 cm^2 white stimulus board laid horizontally on a table. This board consisted of a start button located 10 cm from the edge of the board and a 5 cm grey target zone, which spanned the far edge of the board. Two grey cylinders (24.5 cm tall and 3.5 cm in diameter) could be 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 every trial to prevent participants using the visible holes to guide them.

Liquid-crystal shutter glasses (*Plato*, Translucent Technologies Inc., Toronto, Canada) were worn by participants and were programmed to open for 2 s at the

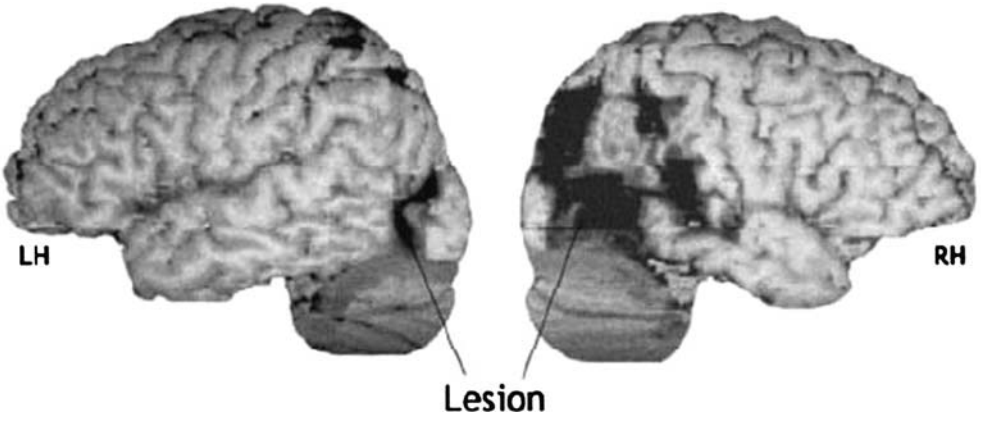

Fig. 4 The lesion sites in patient SB, as reconstructed from MRI scan data. (Reproduced with permission from Lé et al. 2002)

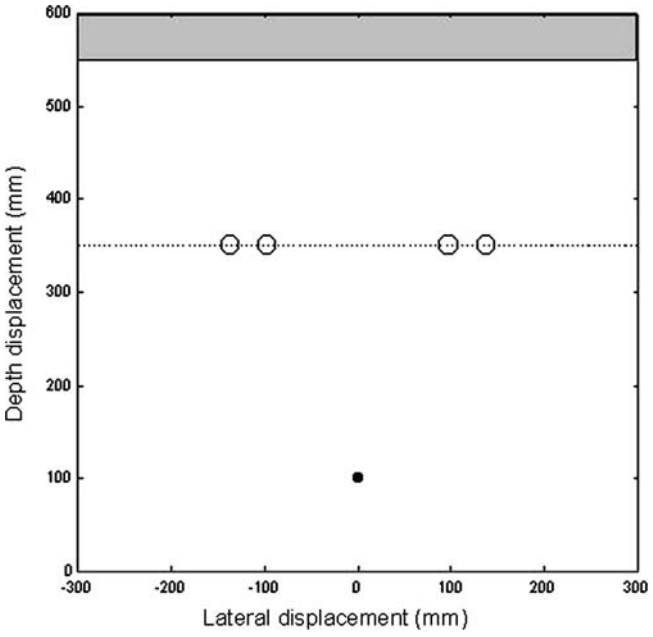

Fig. 5 The experimental arrangement used in Experiment 2. The start button is shown as a *filled black circle*, and the possible locations of the two cylindrical non-target objects are shown as *open circles*. The target zone is shown in *grey* at the far edge of the board. A strip of white card was placed between the two cylinders on every trial to cover the unused holes

onset of each trial. Hand movements were recorded using *Optotrak* (Northern Digital Inc., Waterloo, Ontario, Canada), sampling the position of a marker attached to the nail of the right index finger, at a frequency of 100 Hz. In both the reaching and bisection tasks, the entire movement was recorded (i.e. from the initial start position to the movement endpoint). The start position and end position were defined by the frame at which hand velocity rose or fell below a threshold of 50 mm/s, respectively. The data were processed using custom written Labview programs (National Instruments Inc., Austin, TX, USA).

Procedure

Participants were required to perform both a reaching task and a bisection task, in separate blocks. They were instructed to place their right index finger on the start button when they were ready to begin each trial, and to initiate their response when they heard a tone signal, which was presented immediately on the closure of the shutter glasses. In the reaching task participants were instructed to reach out and touch a target zone located beyond the two cylinders, and were told that the emphasis was on speed of movement. They were instructed that whenever a cylinder was present there would be one on the left and one on the right and they should pass their hand between the two cylinders rather than around the outside edge of the board. Each participant made 60 reaches in a fixed pseudo-random order, with 12 trials for each of the four cylinder configurations and 12 in which no cylinders were present (these trials were included to check for any systematic bias when the reaching response was not constrained by any potential obstacles; they were not included in the main analysis). In the bisection task, participants were informed that the position of the cylinders would vary from trial to trial, and that there would always be one on the left and one on the right. They were instructed to point to the midpoint between the two cylinders, and told that the emphasis in this task was on accuracy of judgement. Each participant made 48 bisection responses, including 12 trials for each of the stimulus configurations, presented in a fixed pseudo-random order.

Results

Analysis

The dependent measure taken for each trial in the bisection task was the final lateral position (P) of the marker on the index finger with respect to the midline of the stimulus board. Similarly, the dependent measure for the reaching task was the lateral position of the marker as it crossed the virtual line joining the two cylinder locations (here the exact value of P was estimated by linear interpolation).

The main analyses were of the weightings given to the two cylinders during each task by each subject (dP_L and dP_R: McIntosh et al. 2004a; Schindler et al. 2004). These indices measure the mean change in P that is associated with a shift of either cylinder between its two locations, while the other remains in the same location (i.e. how much the response shifts in relation to a 40 mm shift of one or the other cylinder). If we denote the four different cylinder locations as a = outer left, b = inner left, c = inner right and d = outer right, 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:

$$dP_L = \text{mean } P(bc, bd) - \text{mean } P(ac, ad)$$
$$\text{[reflecting changes by } a \leftrightarrow b \text{ shifts]}$$
$$dP_R = \text{mean } P(bd, ad) - \text{mean } P(bc, ac)$$
$$\text{[reflecting changes by } c \leftrightarrow d \text{ shifts]}$$

Since there were no significant differences between the two control groups, they were combined in the analyses in order to improve statistical power. The modified t-test recommended by Crawford and Garthwaite (2002) was used to make a statistical comparison between each patient and the combined control group on each of the two indices in each test condition. An independent-samples t-test was also used to compare the group of patients ($n = 2$) to controls ($n = 16$). In a second set of analyses the variability of reaches was assessed by cal-

culating the variance of P. All of the t-tests reported are one-tailed, since they are directional in nature.

Finally the kinematics of the movements were analysed, including reaction time, movement time, peak velocity and time to peak velocity. Reaction time was defined as the time elapsing after the tone signal at which the velocity of the marker attached to index finger rose above 50 mm/s (the start time). Movement time was defined as end time (defined as the time at which the velocity of the marker attached to the index finger fell below 50 mm/s) minus the start time. Peak velocity was defined as the maximum velocity of the marker attached to index finger. Time to peak velocity was the time at which peak velocity occurred, minus the start time. The kinematic data of 11 of the 16 controls were included in the analysis. For the other five control subjects the kinematic data had to be excluded due to technical problems with the trigger sent from the shutter glasses to the *Optotrak* at the time of testing, which caused the timing of the start of the recording to be unreliable. There is no reason to think that the analysed data are unrepresentative of the whole group.

Reaching task

Figure 6 shows the dP_L and dP_R values for each subject in the experiment, that is, the mean changes in reach trajectory (measured as P) that were associated with a 40 mm shift of either the left or right cylinder. It is clear that while a great deal of variability in performance exists among the control subjects, both DF and SB perform within the normal range. The two patients took account of both the left and the right cylinder when making their reaches. Modified t-test comparisons revealed no significant differences between DF and the controls on either dP_L ($t=1.39$, $P=0.092$) or dP_R ($t=0.59$, $P=0.282$). Likewise, there were no significant differences between SB and the controls on either dP_L ($t=0.58$, $P=0.285$) or dP_R ($t=1.05$, $P=0.155$). In addition, an independent-samples t-test carried out on the full data set also failed to reveal any significant difference between the patients ($n=2$) and the controls ($n=16$) on either dP_L ($t=1.38$, $P=0.186$) or dP_R ($t=1.16$, $P=0.263$).

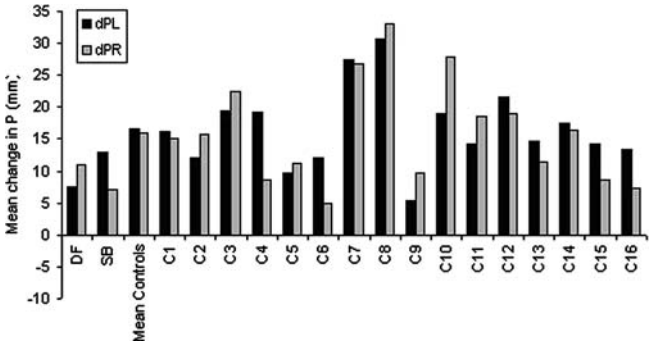

Fig. 6 The 'weightings' (dP_L and dP_R) given to each cylinder by DF and SB and the controls in the reaching task. These *values* indicate the extent to which each subject takes the left or right cylinder's location into account when performing the task

The variance of both patient's P values was higher (DF = 165.8) and (SB = 544.0) than the controls (mean = 131.7). Modified t-tests showed that this difference was significant for SB ($t=3.35$, $P=0.004$), but not for DF ($t=0.28$, $P=0.393$).

Table 2 shows kinematic reaching-task data for DF and SB compared with those of controls. A modified t-test revealed that DF was significantly slower than controls in movement time ($P=0.037$), and that SB differed from controls in the percentage time to peak velocity ($P=0.02$). All other comparisons were non-significant.

Bisection task

Figure 7 shows the mean change in bisection response (P) that was associated with a 40 mm shift of either the left or right cylinder in the bisection task. It can be seen that DF lies outside the control range on both dP_L and dP_R, and that SB lies outside the control range for dP_R, and only just within the lower range of control values for dP_L. Modified t-tests revealed a significant difference between DF and controls on both dP_L ($t=2.51$, $P=0.012$) and dP_R ($t=2.29$, $P=0.019$), and a significant difference between SB and controls on dP_R ($t=1.78$, $P=0.048$). The difference between SB and controls on dP_L failed to reach significance ($t=1.25$, $P=0.116$). Overall independent t-tests revealed significantly lower values in the patients ($n=2$) than in the controls ($n=16$) on both dP_L ($t=2.59$, $P=0.02$) and dP_R ($t=2.87$, $P=0.011$).

The variance of the both patients' bisection points (P-values) was higher than controls (DF = 133.53; SB = 63.67; control mean = 61.39). A modified t-test shows that this was significant for DF ($t=3.55$, $P=0.001$), though not for SB ($t=0.11$, $P=0.456$).

Table 3 shows the kinematic data for the patients and controls on the bisection task. Modified t-tests revealed significantly lengthened movement times in both DF ($P=0.027$) and SB ($P=0.033$). Both DF ($P=0.04$) and SB ($P=0.004$) also differed from the controls in time to peak velocity, but this was due to their longer movement durations, and the differences disappeared when time to peak velocity was taken as a percentage of movement time. All other comparisons were non-significant.

Table 2 Experiment 2: kinematic data for DF, SB and 11 healthy control subjects in the reaching task

Subject	RT (ms)	MT (ms)	PV (mm/s)	TPV (ms)	%TPV
DF	448.75	932.46*	1203.43	351.46	37.56
SB	351.25	439.17	2926.58	220.74	50.26*
Mean C	206.85	603.45	1742.98	238.56	39.46

*$P < 0.05$

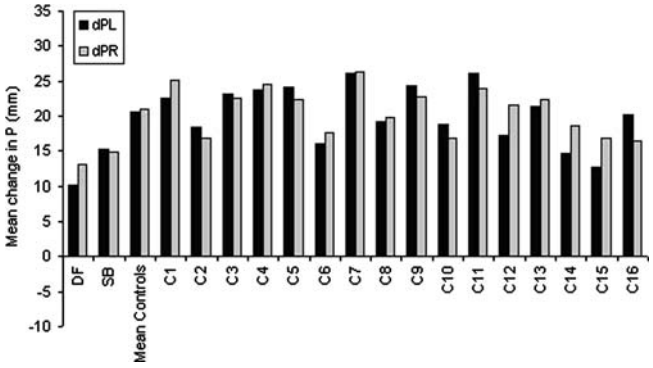

Fig. 7 The weightings given to each cylinder by DF and SB and the controls in the bisection task

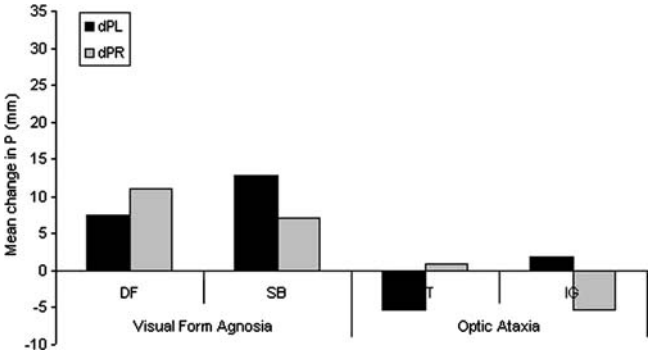

Fig. 8 The weightings given to the two cylinders by our two visual form agnosic patients (DF and SB) and by optic ataxic patients AT and IG (Schindler et al. 2004) in the reaching task

Discussion

The aim of Experiment 2 was to examine obstacle avoidance behaviour in two patients with bilateral ventral stream damage resulting in visual form agnosia, when they were asked to reach between two cylinders varying in location from trial to trial. The results show that our patients shifted their reaching trajectories in response to shifts in obstacle position to an extent that fell within the normal range. Nevertheless, the patients both failed to shift their bisections of the space between the same two objects from trial to trial to the same extent as control subjects. As shown in Figs. 8 and 9, these results provide a partial double dissociation when taken in combination with those from the two optic ataxic patients tested by Schindler et al. (2004). We believe that this contrast provides strong evidence to support the role of the dorsal stream in automatic obstacle avoidance. It should be noted, however, that there are differences in the way the two groups of patients were tested—the optic ataxia patients were required to maintain central fixation during the tasks whereas the visual form agnosic patients were allowed free vision. This difference in testing conditions was due to the fact that SB suffers from hemianopia in his left visual field, and we wanted to ensure that he could see both of the obstacles.

In the bisection task there was no significant difference between SB and controls in the weightings attached to the left pole. This may perhaps be explained by the fact that SB has acquired, as a result of his left hemianopia, a compensatory strategy of habitually paying more attention to the left than the right side of space. He could have done this easily in the present task through overt scanning, since there was no requirement to fixate centrally while initially viewing the array. Indirect evidence for this possibility is that SB tended to take long reaction times prior to lifting his finger from the start switch (particulary in the bisection task). Also, it is notable that despite his left visual hemifield being 'blind', SB's responses are more heavily influenced by the left cylinder than the right in both the reaching and bisection tasks. (In contrast, in a separate reaching experiment in which SB was required to fixate on a central target during the viewing period, his responses showed little influence of shifts in the left cylinder, his dP_L value dropping from the present 12.86 mm to a non-significant 3.83 mm.)

The major prediction of this study was that their functionally intact dorsal streams should allow both DF and SB to perform normally in the reaching task, where no perceptual judgements were required. The prediction as to how they would perform in the bisection task, however, was less strong, since neither

Table 3 Experiment 2: kinematic data for DF, SB and 11 healthy control subjects in the bisection task

Subject	RT (ms)	MT (ms)	PV (mm/s)	TPV (ms)	%TPV
DF	431.46	948.44*	564.1	425.42*	44.85
SB	580.21	930.63*	682.86	538.57**	57.87
Mean C	349.2636	602.71	907.6009	267.7645	45.47

*$P < 0.05$; **$P < 0.005$

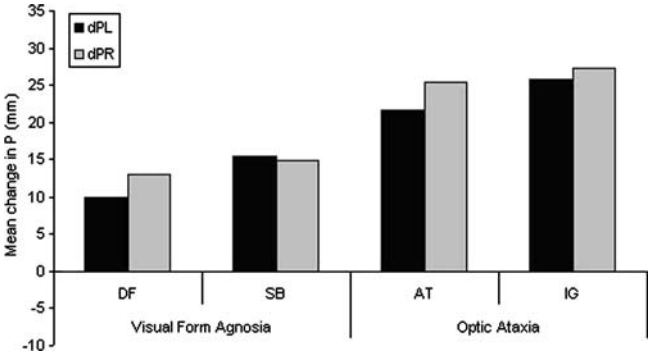

Fig. 9 The weightings given to the two cylinders by our two visual form agnosic patients (DF and SB) and by optic ataxic patients AT and IG (Schindler et al. 2004) in the bisection task

has a totally destroyed ventral stream. James et al. (2003) demonstrated that the ventral stream lesions in DF are largely restricted to area LO, though the damage is larger in the right hemisphere than the left. The primary visual cortex as well as lingual and fusiform gyri are largely spared. Studies by Steeves and colleagues have shown that there is sparing of DF's fusiform face area (Steeves et al. 2006) as well as of her parahippocampal place area (Steeves et al. 2004). Such spared ventral stream areas could be implicated in spatial perception in healthy individuals, and this could explain some of DF's preserved abilities in the bisection task. A close look at SB's lesion reveals a similar sparing of ventral stream areas, particularly in the left hemisphere, which may account for some of his preserved abilities in the bisection task. In sum, it is clear that neither patient has a completely destroyed ventral stream, and therefore it would be unlikely that either patient would be totally unable to perform the bisection task. In practice, both of them did perform at above-chance levels.

While the variability of the patients' responses was higher than that of controls in both tasks, this cannot explain the absence of a statistically significant deficit in the reaching task, for several reasons. First, the calculation of the weightings attached to the change in position of the left and the right cylinder was based only on mean reach trajectories, and as such would not have been affected by the variability of responses. Second, while both patients tended to have higher variability of responses than controls in both tasks, the difference was small and non-significant for DF in the reaching task (and for SB in the bisection task). Finally, if variability of responses could explain the data it is unlikely that a dissociation between the two tasks would have emerged, since it was present in both tasks.

The results of the kinematic analyses are consistent with our conclusions, in that overall the patients showed greater deficits on the bisection task than the reaching task. Both moved significantly more slowly than controls on the bisection task, whereas DF only did so during the reaching task. Of course the slower movement times in the bisection task cannot themselves explain the deficits seen in that task: if anything one would expect a speed-accuracy trade-off. In general the control subjects showed greater dP_L and dP_R values on the bisection than the reaching task, which is in agreement with previous work (McIntosh et al. 2004a; Schindler et al. 2004). In part this may have been due to the differential instructions given to participants, which were also reflected in the longer reaction times and movement times, and lower peak velocities, on the bisection task than the reaching. Presumably the kinematics of the patients' behaviour too reflected these different task demands.

It is important to note that while DF and SB both show visual form agnosia, there are distinct differences between them in their pathology and associated deficits. For example, DF detects high spatial frequencies well, whereas SB performs better at low spatial frequencies; and DF has relatively preserved colour vision, whereas SB is achromatopsic (Lê et al. 2002). SB's right ventral stream damage is more extensive than DF's, and his right parietal lesion is more extensive than DF's left parietal lesion. On the other hand DF has associated sulcal widening that is less apparent in SB, and she sustained her brain damage in adulthood rather than childhood. Finally, SB's extensive right hemisphere (including white matter) damage has resulted in a hemianopia in his left visual field, whereas DF has a smaller lower visual-field scotoma. The remarkable thing is that despite all of these differences, the two patients behaved in a comparable fashion in our two tasks.

Conclusions

In Experiment 1, DF shifted her trajectory and adjusted her grip aperture in the same manner as controls when asked to reach and grasp a target object in the presence of non-target objects. In Experiment 2, both DF and SB shifted their trajectories with respect to shifts in cylinder location when asked to reach between two non-target objects in the same way as the controls, while showing a reduced influence of the same two objects when required to make an explicit bisection judgement between them. We interpret these results in terms of automatic obstacle avoidance, and conclude that this implicit skill, whereby movement programming is modified as a function of non-target objects, is preserved in patients with ventral stream damage.

In line with our previous findings with neglect patients (McIntosh et al. 2004a) and optic ataxic patients (Schindler et al. 2004), we believe that the present data provide further convergent support for the view that automatic obstacle avoidance is a function of the dorsal stream of visual processing. When this system is damaged, the automatic motor adjustments that we have been measuring are absent; whereas when either the ventral stream or the temporo-parietal systems associated with spatial neglect are damaged, these adjustments remain intact. Our results extend the functional description of the ventral and dorsal streams that has been developing over recent years (Milner and Goodale 1995; Goodale and Milner 2004). Not only is the dorsal stream intimately involved in the transformation of target properties such as size and location into motor coordinates for programming and controlling reaching and grasping movements, it also automatically takes into account the location of non-target stimuli while carrying out these computations.

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