Covert processing of visual form in the absence of area LO

R. W. Kentridge*, C. A. Heywood, A. D. Milner

Department of Psychology, Cognitive Neuroscience Research Unit, University of Durham, South Road, Durham DH1 3LE, UK

Abstract

The patient D.F., who suffers from severe visual form agnosia, has been found to have a bilateral lesion of area LO, an area known to be intimately involved in the perception of object shape. Despite her perceptual impairment, however, D.F. retains residual form processing abilities that can provide distal visuomotor control, for example in the configuration of her grasp when reaching to pick up objects of different shapes and sizes. This dissociation has been interpreted as reflecting the sparing of a dedicated system for processing the physical properties of objects solely for purposes of guiding action. Here we test this hypothesis in two studies designed to examine whether or not spared shape processing capacities might be revealed under other kinds of indirect test conditions. First, we exploited the fact that a redundant shape cue will speed search for a coloured stimulus within an array, and vice versa. Unlike our control subjects, D.F. showed no facilitation effect of either kind. Second, we used two Stroop tasks in which single coloured uppercase letters were presented. Our intention was to determine (a) whether naming the colour would be influenced by whether the letter was the initial letter of the correct or incorrect colour name (e.g. 'R' or 'G'); and (b) whether the reverse might be true, that is that D.F.'s guesses at letter identity might be influenced by their colour. We found no evidence for a Stroop effect of the former (standard) kind in D.F., but we did find evidence for reverse-Stroop effects. This result may reflect a partial sparing of ventral stream areas specialised for letter-form processing.
© 2004 Elsevier Ltd. All rights reserved.

Keywords: Implicit; Visual; Shape perception; Visual agnosia; Visual streams

1. introduction

Visual form agnosia is a neurological disorder of visual perception which manifests itself in the laboratory as an impairment in making judgements about the shape of visually presented stimuli. A patient with a particularly clear-cut example of this condition, D.F., has been studied extensively over a 15 year period, because of the insights her behaviour has provided into the organisation of visual processing in the normal human brain. It has been shown that D.F., who cannot give correct reports of the shape, size or orientation of simple visual stimuli, nevertheless makes entirely appropriate manual responses to their physical characteristics, showing for example appropriate anticipatory hand shaping and digit positioning while reaching to grasp them (Milner et al., 1991; Goodale, Milner, Jakobson, & Carey, 1991; Goodale et al., 1994). In conjunction with complementary evidence from another neurological deficit, optic ataxia, these data strongly support the view that the processing of visual information for the purposes of action and for the

purposes of object identification have anatomically distinct bases (Milner & Goodale, 1995).

In particular, Milner and Goodale (1995) hypothesised that perceptual processing and the online visual guidance of action were linked with the two broad divisions of the cortical visual system (Ungerleider & Mishkin, 1982): the occipito-temporal "ventral" stream and the occipito-parietal "dorsal" stream, respectively. Recent detailed examination of D.F.'s brain using magnetic resonance imaging lends support to this interpretation. First, high-resolution structural MRI has revealed that D.F.'s lesions have bilaterally destroyed a region that corresponds closely to the location in healthy control subjects of the lateral occipital area (LO: Malach et al., 1995; Kourtzi & Kanwisher, 2000). This brain area is defined by the difference between the activation pattern elicited by images of objects and the pattern elicited by fragmented versions of those images, and it may be approximately homologous with TE/TEO in the monkey's ventral stream (Malach et al., 1995; Tanaka, 1997; Tootell, Tsao, Vanduffel, 2003). When D.F. was presented with images of intact and fragmented line drawings of objects, she showed no net activity at all in her ventral stream (James, Culham, Humphrey, Milner, & Goodale, 2003). Together, these new studies suggest strongly that it is the bilateral loss

---
* Corresponding author. Tel.: +44-191-334-3261;
fax: +44-191-334-3241.

E-mail address: robert.kentridge@durham.ac.uk (R.W. Kentridge).

of area LO that has precipitated D.F.'s visual form agnosia. In contrast to her ventral-stream dysfunction, when D.F. was scanned while reaching to grasp a series of oriented rectangular blocks, she showed clear activity in the anterior intraparietal area of the dorsal stream (AIP: Binkofski et al., 1998; Culham et al., 2003).

Milner and Goodale have interpreted their findings in D.F. as reflecting a non-functioning system for shape *perception*, but a functioning system for shape processing for action (Milner & Goodale, 1995; Goodale & Milner, 2004). In other words, their suggestion is that the implicit shape processing shown by D.F. is only available for purposes of guiding action. No shape processing should be available for playing any role in the perceptual processing of the ventral stream. A recent report by Aglioti, Bricolo, Cantagallo, and Berlucchi (1999) on another patient with visual form agnosia provides partial confirmation of this hypothesis. Their patient (S.F.) could not name objects, and failed in formal tests of object form discrimination. Like D.F., however, (Milner & Heywood, 1989), the patient retained the ability to recognise and name colours. This allowed them to construct a test for *implicit* visual perception of shape. Aglioti and his colleagues used two variants of the classic Stroop effect in order to look for an implicit effect of form on the responses of their patient. They first used the standard Stroop task, in which the reaction time for a subject to identify the colour of a stimulus is increased if the stimulus is the word for a different colour. For example, subjects are slower to respond 'green' to the word 'red' printed in green ink than they are to green-ink presentations of the word 'talk', the non-word 'vulp' or the character string 'xxxx'. Aglioti et al. (1999) used a reduced version of this task, in which the stimuli were the initial letters of the words 'red' and 'green', 'R' and 'G', which could be written in red or green ink (their subject was Italian, so in fact they used 'R' and 'V', the initial letters of 'rosso' and 'verde'). They found no effects of letter/colour congruity on either accuracy or speed of reactions in the classic colour naming Stroop task.

Although Aglioti and colleagues found no evidence for covert access to form information in S.F. using the standard Stroop task, they did find a curious positive result using a reverse version of the task. In the reverse-Stroop task, the subject must name the word rather than the ink colour. Again, an incongruity between a word's colour and its semantics retards reaction time, although to a much lesser extent than in the classic Stroop task (see Macleod, 1991 for a review). On the face of it, one would expect a visual form agnosic to be incapable of this reverse-Stroop task, because s/he would not be able to identify the words to which they had to respond. Aglioti et al., however, found effects both on accuracy and reaction time in the reverse-Stroop letter identification task, despite the fact that the patient performed steadfastly at chance when asked to name the letters presented in black on white (see also Berlucchi, 2003). They suggest that the colour of the stimulus elicited a representation with associations to the colour name, and that this representation

might exert a top–down influence to amplify an imperfect but partial processing of stimulus form within the ventral stream. This might then raise the probability of appropriate letter identification above chance when the letter was presented in a congruent colour, even though the subject still reported that their responses were guesses. This effect was not one of implicit form perception, but rather one that appeared when the patient explicitly paid attention to stimulus form.

Our aims in this paper are twofold. We wish to see whether the reverse letter-naming Stroop task is also capable of revealing hitherto unidentified residual form processing abilities in D.F. not specifically engaged in the service of action. We also wish to investigate whether a task-irrelevant colour cue can also facilitate form processing in a task that does not draw on long-term memories for colour-form associations such as those between colours and the initial letters of their colour-words. In our first experiment, we report the results of experiments in which D.F. either had to search among an array of coloured shapes for a target item matching the colour of a previously shown sample or had to search among an identical array of coloured shapes for a target item matching the shape of the sample. We had found in pilot studies that healthy subjects showed improved search times in both tasks when the task irrelevant feature, be it shape or colour, was common to the sample and the target. This task can be seen as one in which associations to properties held in working memory, rather than long-term memory, influence a performance despite the fact that attending to those properties does not aid in execution of the task. In this sense it is an analogue of forward and reverse-Stroop tasks where irrelevant properties of letter-form or letter-colour influence discrimination of the colour or letter, respectively. Our second and third experiments test two variants of forward and reverse single letter Stroop tasks in replication of Aglioti et al. (1999).

2. Subjects

D.F. was aged 46 (shape part of Experiment 1, plus Experiment 2) and 48 (orientation part of Experiment 1, plus Experiment 3) at the times of testing. Her clinical picture has been described in detail elsewhere (Milner et al., 1991; Goodale & Milner, 2004), including MRI scans of her brain damage (Milner et al., 1991; James et al., 2003). At the times of testing, respectively 12 and 14 years after incurring her brain damage, D.F. continued to show severe visual form agnosia, although her condition has improved over the years. To a large extent this improvement is probably due to acquired skills such as self-cueing from her functioning visuomotor system (Murphy, Racicot, & Goodale, 1996; Dijkerman & Milner, 1997), rather than to a genuine improvement in perception (Goodale & Milner, 2004).

In Experiment 1, we also tested 15 healthy control subjects, all students or staff of the University of Durham.

3. Experiment 1

3.1. Methods

In each of two tasks, subjects were briefly presented with a sample stimulus, followed by a set of five stimuli, and the subject had to indicate whether any of these five stimuli matched the sample. The search property to be matched was either form or colour, the other dimension being irrelevant to the task. Target stimuli were actually present on 50% of trials. On half of these occasions (25% of the whole set of trials) the target matched the sample in both the task dimension and the irrelevant dimension, while in the other target trials (25% of the whole set) the target matched the sample in the search dimension, but not in the other dimension. We tested D.F. on two versions of the experiment, one with colour and shape as the two dimensions, and the other with colour and orientation as the two dimensions. Four blocks of 64 trials were conducted for each task.

Stimuli were produced using a Cambridge Research Systems VSG 2/3 graphics system and displayed on an Eizo F784 21″ colour monitor calibrated using a Cambridge Research Systems ColorCal chromameter and checked using a Minolta LM-100 photometer. Responses were recorded with a Cambridge Research Systems CB2 button-box.

Three different shapes, each in two orientations, were used in the 'shape' version of the experiment. The shapes were a $1° \times 2°$ rectangle oriented horizontally or vertically, an isosceles triangle of base $2° \times$ height $1°$ with the apex pointing either upwards or downwards and a hemi-circle from a disc of radius $2°$ with the curved edge pointing either upwards or downwards. For the 'orientation' version of the task the stimuli were $0.3° \times 1.8°$ bars oriented at 0, 30, 60, 90, 120 or $150°$ to the vertical. Six colours were used to draw the stimuli. These colours were taken from equally spaced angles around a colour circle in L, u', v' colour space (a colour-space in which colours at equal distances are approximately equally discriminable from one another), centred on the grey point [CIE(x, y) coordinates 0.33, 0.33] with an L, u', v' eccentricity of 0.1, yielding the following colours:

u'	v'	Colour
0.3103	0.4795	Pink
0.2554	0.5630	Orange-yellow
0.1555	0.5572	Lime-green
0.1107	0.4678	Turquoise
0.1657	0.3843	Lilac
0.2655	0.3901	Magenta

All colours had a luminance of $20 \, cd \, m^{-2}$, and the black background had a luminance of $0.2 \, cd \, m^{-2}$.

At the start of each trial, the sample stimulus was presented for 1 s at a point on the vertical meridian and $7°$ above the horizontal meridian. It was then replaced by the search array of five stimuli arranged pseudorandomly within an area from $5°$ to the left of the midline on the horizontal meridian, to $5°$ to the right of the midline and $5°$ below the horizontal meridian. The locations were chosen so that the minimum spatial separation between stimuli was $1°$. The search array remained present until a response indicating the presence or absence of a target was made. The response was accompanied by a tone from the button-box. The next trial started after a 1.5 s inter-trial interval.

3.2. Results

The dependent measure was the mean reaction time for correct responses to trials with a target present, and the question was whether search was speeded by having a second stimulus property common to both sample and target stimulus. Fig. 1a depicts the results when the search target was defined by shape. There was no effect of colour-congruence [$t(54) = 0.052$, n.s.]: that is, D.F. was no quicker to find the target when it shared colour as well as shape with the sample. D.F., however, responded correctly on only 28/64 (44%) incongruent trials with a target present and 28/64 (44%) congruent trials with a target present. Congruence clearly did not affect accuracy, but accuracy did not differ from chance.

Fig. 1b shows the effect of shape congruence on colour search, the main comparison of interest in this experiment. Shape congruence did not affect the speed of search [$t(105) = 0.530$, n.s.] nor its accuracy [55/64 (86%) incongruent, 52/64 (81%) congruent; Fisher exact $P = 0.147$]. Thus there was no evidence either for above-chance discrimination of shape (in the shape search task), nor for any effect of shape congruence on colour search, although this was reasonably accurate.

Fig. 2a shows the effects of colour congruence on orientation search times. Again colour congruence did not affect the speed of search [$t(67) = 0.913$, n.s.] nor its accuracy [37/64 (58%) incongruent, 32/64 (50%) congruent, Fisher exact $P = 0.096$], which again did not exceed chance performance. Similar results as before were found for colour search (Fig. 2b): there was no significant effect of orientation congruence on the speed of search [$t(95) = 0.236$, n.s.] nor on its accuracy [49/64 (77%) incongruent, 48/64 (75%) congruent, Fisher exact $P = 0.16$].

For healthy observers, irrelevant matches in the non-task dimension were found to speed both colour-matching and form-matching tasks. Subjects were discarded from analyses if their error rates exceeded 10%. Harmonic mean reaction times were then computed for each subject's correct responses in each condition. Paired t-tests show a significant reaction time advantage for congruent targets in both the shape matching task [$t(11) = 5.079$, $P < 0.001$; colour-congruent mean RT 746 ms, colour-incongruent mean RT 860 ms], and the colour-matching task [$t(12) = 4.325$, $P < 0.001$, shape-congruent mean RT 694 ms, shape-incongruent mean RT 742 ms].
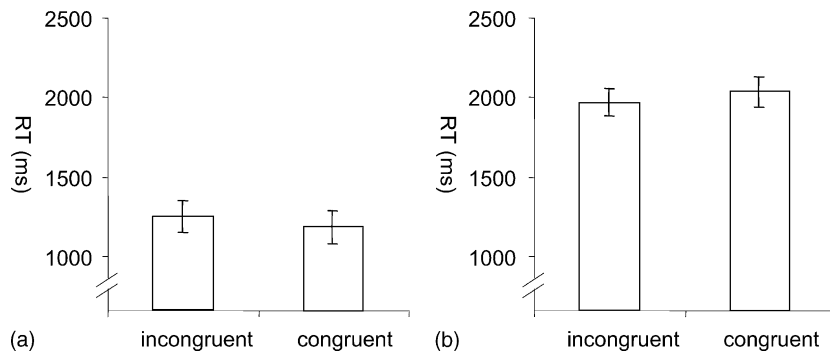
Fig. 1. Experiment 1: (a) the effect of colour congruence on shape search; (b) the effect of shape congruence on colour search. Mean RTs and standard errors are shown. In neither task was there any significant effect.
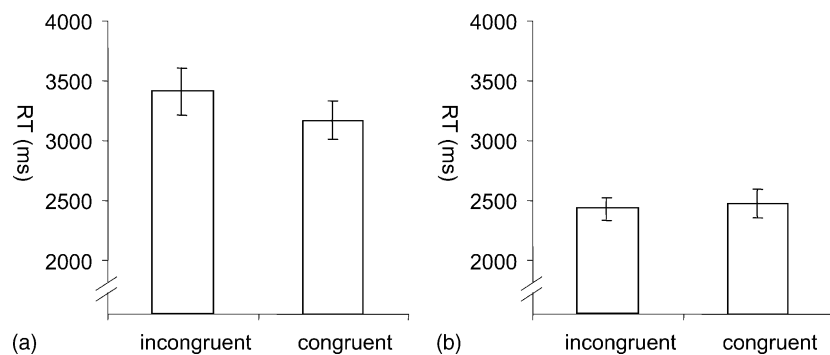

Fig. 2. Experiment 1: (a) the effect of colour congruence on orientation search; (b) the effect of orientation congruence on colour search. Mean RTs and standard errors are shown. In neither task was there any significant effect.

4. Experiment 2

4.1. Methods

The subject was presented with one of two letters on a display screen, an uppercase 'R' or 'G', with each letter in one of two equiluminant colours. The letters were presented in a 72-point Arial font. They measured 3.6° high, and the maximum width of both the 'R' and 'G' was 3.9°, though the width of the closed loop at the top of the 'R' was only 3.4°. The colours used were $26.0 \, \text{cd m}^{-2}$ red and green with CIE(x, y) coordinates (0.624, 0.342) and (0.276, 0.611), respectively, set against a $0.2 \, \text{cd m}^{-2}$ black background.

The four letter-colour combinations were scheduled with equal frequency and in pseudorandom sequence. Trials began with a short warning tone, with the stimulus letter then appearing at a location varying randomly from trial to trial within an 8° square area at the centre of the screen. The subject's task was to press as quickly as possible one of two keys presented side by side on the button-box in order to report her decision on the letter's colour or its identity (in different experiments). Testing was conducted in blocks of 64 trials.

D.F. completed two versions of the single letter Stroop task. In the first four blocks, her task on each trial was to report whether the stimulus was coloured red or green

(the normal Stroop task). In the second set of four blocks (conducted the following day) her task was to report (if necessary by guessing) whether the letter presented was an 'R' or a 'G' (reverse-Stroop task). In all cases we discarded any RTs more than two standard deviations away from the mean prior to analysis.

4.2. Results

In the standard Stroop task, D.F. made no errors of colour identification, as would be expected from her largely preserved colour perception. Yet her reaction times to name the colours were quite unaffected by the congruence between letter and colour [$t(246) = 0.837$, n.s.]. Mean RTs and standard errors are shown in Fig. 3. Evidently there was no influence at all of the identity of the letter on her colour-naming performance, thus again providing no evidence for implicit shape perception.

In the reverse-Stroop task, the data were more complex. Unlike Aglioti et al.'s patient S.F., D.F. proved able to discriminate between the 'R's and 'G's to some extent, whether they were congruently or incongruently coloured. In both cases, however, she responded incorrectly more often than correctly. She was incorrect on 86/128 (67%) of incongruent trials and 70/128 (55%) of congruent ones. This difference just fails to reach significance either on a
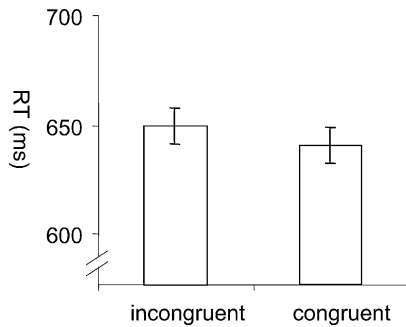
Fig. 3. Experiment 2: mean RTs and standard errors for naming colours in a red/green Stroop task. There was no significant difference between congruent and incongruent trials.

Fig. 5. Experiment 3: mean RTs and standard errors for naming colours in a blue/green (b/g) Stroop task. There was no significant difference between congruent and incongruent trials.

chi-square test [$\chi^2(1) = 3.692$, $P = 0.055$ with continuity correction] or on a Fisher exact probability test ($P = 0.054$). D.F.'s average level of performance (100/256, 39% correct) was significantly worse than chance, although separate assessment showed this to be true only of the incongruent trials (33% correct; binomial two-tail $P < 0.0001$). No Stroop effect was evident when the RTs on the incorrect trials were analysed [$t(146) = 1.289$, n.s.], as shown in Fig. 4a. As shown in Fig. 4b, however, there was a significant Stroop effect on the minority of correct trials [$t(95) = 3.389$, $P = 0.001$].

As D.F. was clearly discriminating better than chance, though responding incorrectly, we then tried providing verbal feedback (correct/incorrect) for a small number of trials. She reported that although she felt she could tell the difference between the two types of stimuli (one was "taller and thinner than the other") she was unsure which was which. After this feedback training, she completed two blocks of trials where the letters were all coloured orange (a 50:50 mixture of the previous red and green colours), and she now responded correctly on 99/128 (77%) of trials.

5. Experiment 3

We repeated Experiment 2, but now using the lowercase letters 'b' and 'g' presented in equiluminant blue and green, instead of the red and green 'R's and 'G's used in Experiment 2. The reason for using this new task was that we wished to use letter stimuli that D.F. could not distinguish explicitly. This would be necessary in order to use Stroop data to argue for any *implicit* interference or facilitation effects of letter form on colour judgements, and also in order to replicate the results of Aglioti et al. (1999) on the reverse-Stroop task.

5.1. Methods

The 'b' and 'g' stimuli were presented, as before, in a 72-point Arial font. The letters measured 3.6° high, and the maximum width in both cases was 3.0°. The colours used were 14.0 cd m^{-2} blue and green with CIE coordinates (0.150, 0.065) and (0.276, 0.611), respectively, presented against a 0.2 cd m^{-2} black background. In all other respects the stimuli and procedures used were identical to those of Experiment 2.
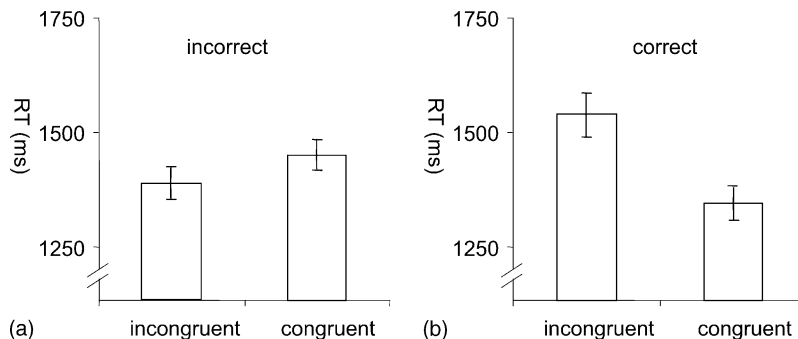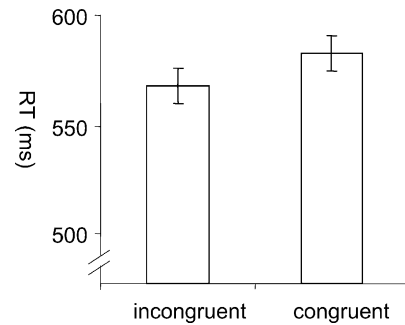

Fig. 4. Experiment 2: mean RTs and standard errors for naming letters in a red/green (R/G) Stroop task. (a) There was no significant difference between congruent and incongruent RTs on incorrect trials (which were the majority), but (b) there was a significant difference between congruent and incongruent RTs on correct trials.
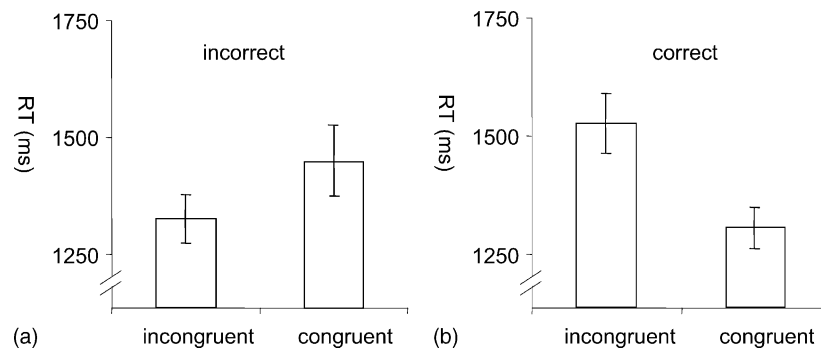
Fig. 6. Experiment 3: mean RTs and standard errors for naming colours in a blue/green Stroop task. (a) There was no significant difference between congruent and incongruent RTs on incorrect trials, but (b) there was a significant difference between congruent and incongruent RTs on correct trials.

5.2. Results

On the standard Stroop colour identification task, D.F. made only two errors, which were subsequently discarded. Analysis of her latencies again revealed no significant standard Stroop effect, as shown in Fig. 5 [$t(240) = 1.306$, n.s.]. On the reverse-Stroop task, D.F. discriminated significantly and now correctly (73/128: 57% correct) between 'b's and 'g's when they were congruently coloured. Her responses to incongruently coloured stimuli were predominantly incorrect (54/128: 42% correct). On a 2×2 χ^2 test this difference is significant [$\chi^2(1) = 5.063$, $P = 0.024$ with a continuity correction; Fisher exact test $P = 0.024$]. Overall, however, D.F.'s performance (127/256) is at chance, indicating that she was unable to distinguish the two letters explicitly. Indeed, when she was tested with neutrally coloured 'b's and 'g's (using an equal mixture of the blue and green), D.F. discriminated correctly on only 135/256 (52.7%) of trials, which does not differ significantly from chance.

These percentage correct data alone could be explained as resulting from a response bias of the kind "respond 'b' when the letter is blue, and 'g' when it is green", without any need to assume that shape was being discriminated. However, analysis of her reaction times allows us to discount this interpretation. Here again D.F. showed a strong reverse-Stroop effect [$t(123) = 2.966$, $P = 0.004$] on trials where she responded correctly (see Fig. 6b). No significant Stroop effect is apparent, however, when her incorrect trials are considered [$t(122) = 1.399$, n.s.], as illustrated in Fig. 6a.

6. Discussion

What do these studies tell us about the nature of D.F.'s visual form agnosia? In all three experiments, our indirect tests, in which D.F. was asked to respond to the *colour* of stimuli failed to reveal any evidence for implicit processing of form. We did, however, find the reverse effect in Experiments 2 and 3—the colour of stimuli did influence performance in form discrimination tasks. This is in full agreement

with the failure of Aglioti et al. (1999) to find evidence of standard Stroop effects in their patient S.F. and their demonstration of a reverse-Stroop effect in the same patient. Our first experiment, however, gave no indication of any residual processing of stimulus shape or orientation for target identification in a task of explicit search for form. D.F. was quite unable to search successfully for a particular shape or orientation she had been shown as the sample, and colour congruence had no effect on her accuracy or speed in this task. In normal observers task-irrelevant colour did affect the speed with which items matching the sample were detected, suggesting that automatic processing of colour was unavoidable and aided target detection.

We can contrast these negative findings with the clear reverse-Stroop effects found by Aglioti et al. (1999), which we too found in Experiments 2 and 3 and discuss in detail in the following paragraphs. There are of course a number of potentially critical differences between our search tasks and the reverse-Stroop task. First, it must be stressed that the search tasks impose demands beyond the discrimination of specific forms. The target shape, and the target colour, if it is to have any effect on performance, must be held in working memory during visual search (although we attempted to minimise the cost using the shortest possible, single-frame, delay between target offset and search array onset). Our failure to find an effect with D.F. in this task might, therefore, reflect a deficit in encoding form into visual working memory rather than an absence of residual form *recognition* abilities per se. It may also be the case that a shape-matching task with five alternatives in the search array is inherently harder than a two-alternate discrimination task using once familiar letter stimuli. Alternatively, however, it may be that letter processing takes place in brain areas outside those used in the processing of shape per se or those used in the recognition of objects. The results of the reverse-Stroop tasks in Experiments 2 and 3, which used only letters, may therefore provide clues as to the differential processing of shapes and letters within the ventral stream.

The first aspect of the data from the reverse-Stroop tasks that must be discussed is D.F.'s ability to discriminate *explicitly* between uppercase 'R's and 'G's. This was initially

manifest as significantly *below*-chance performance in the reverse-Stroop task, where she was asked to guess at letter identity when the letters were presented in congruent or incongruent colours. However, when she was given feedback about the correctness of her guesses, she was able to turn this into a clearly *above*-chance rate of correct guesses. D.F. protested that she was merely guessing throughout, though she did admit to a feeling that the letters differed in the 'tall and thin' dimension. They were actually of equal height and maximum width, and differed in area by less than 2%. Inevitably, they did, however, differ in a variety of low-level properties that it may be possible to exploit in the absence of true form perception. For example, the letter 'G' turns out to have approximately equal power after convolution with vertically or horizontally oriented filters, whereas the letter 'R' produces much more vertical power than horizontal. Thus although D.F. could not be said to have demonstrated shape perception in this task, at least she seems to have been able to latch on to some rudimentary property of these stimuli. When in Experiment 3 we used lowercase 'b's and 'g's, her ability to discriminate fell to chance. D.F.'s latencies to report on both 'R' versus 'G' and 'b' versus 'g' letter discriminations were of the order of 1500 ms, about twice the time she needed her to make colour discriminations. This would be consistent with her assertion that her letter-shape decisions were not based on conscious discrimination (as they were in the colour task) but truly were (educated) guesses.

Strong effects of letter-colour congruity were exhibited by D.F. on both of our two reverse-Stroop tasks. These effects bear a strong similarity to the data reported previously by Aglioti et al. (1999) on their patient S.F. The most surprising aspect of these effects emerged in the red/green reverse-Stroop task, in which D.F. was partially able to discriminate 'R's from 'G's, but did so *incorrectly*. Yet despite this below-chance performance, the reverse-Stroop effect was only evident on the minority of trials where she responded *correctly*. There was no reverse-Stroop effect on the incorrect trials, although one might have expected to find a negative effect there if the letter 'R' was eliciting a representation of greenness and the letter 'G' one of redness. The strong positive reverse-Stroop effect found on the correct trials indicates that responding R to 'R's and G to 'G's must have been affected by colour-appropriate associations on those trials, but that these covert effects were not strong enough to drive D.F.'s overt responses on a majority of trials. We suppose that these overt responses were driven by an entirely superstitious association of colour identity with some low-level visual feature of 'R's or 'G's. The fact that the covert letter representation elicited by the letters and revealed by the reverse-Stroop effects and the overt, if superstitious, visual identification of the letters could act independently of each other thus suggests that the veridical covert representation was not part of the same visual letter identification process mediating D.F.'s overt visual discrimination.

In Experiment 3 the letter stimuli 'b' and 'g' were not discriminable explicitly by D.F., either when congruent and incongruent trials were pooled, or when colour was not available as a differential cue. This task therefore provides a close analogue to the 'R' versus 'G' task used with patient S.F. by Aglioti et al. (1999). D.F.'s responses to 'b's and 'g's were now above-chance when appropriately coloured, and below-chance when inappropriately coloured. The reverse-Stroop effect was again found only on correct trials, exactly as in Aglioti et al.'s report. Presumably when tested with the 'b's and 'g's, D.F. was not able to use whatever low-level feature might have been permitting discrimination between 'R's and 'G's.

The clear reverse-Stroop effect that we found (both in terms of percent correct and reaction times) suggests that there really was some genuine processing of the shapes of letters in D.F. Aglioti et al. (1999) surmised that the colour of the stimulus elicited a semantically-rich representation that included associations to the colour name, and that this representation could exert a top–down influence on perceptual processing. Evidently D.F. too has some spared capacity, despite her bilaterally damaged area LO, to process letter shape at sub-threshold level, and this activity can be facilitated or interfered with by top–down semantic influences.

Two interpretations of these data in terms of specialised processing areas for letters are possible. First, it has been suggested that there may be distinct brain regions for visual processing of words or letters and for processing of objects (e.g. Polk & Farah, 1998; Polk et al., 2002). It is possible that D.F.'s damage in the vicinity of area LO spares enough of a specialised visual letter processing area (e.g. in left-hemisphere inferior occipitotemporal cortex near the fusiform gyrus) to support visual letter recognition aided by top–down cues derived from associations with colour. This interpretation is consistent with D.F.'s performance when given object recognition tasks. She performs consistently better when provided with additional cues such as colour, shading, and visual texture, than when given plain outline drawings (Humphrey, Goodale, Jakobson, & Servos, 1994). We now know from functional MRI studies that these surface cues result in scattered ventral-stream activations in D.F. where none exist otherwise (James et al., 2003). We assume that top–down processes are always at work in object recognition tasks, and that perhaps in D.F. these are able to activate ventral-stream networks that extend beyond area LO.

The second, slightly different, interpretation would be that the overlap between specifically visual letter and object recognition areas is too great to allow such sparing (see e.g. Joseph, Gathers, & Piper, 2003). Instead, letter processing in areas remote from LO, such as the area in inferior parietal cortex normally used in the service of phonological recoding and activated by visual stimuli, may mediate reverse-Stroop effects in D.F. and S.F. This notion is attractive for two reasons. First, it is easier to reconcile the dissociation between overt visual letter (mis)identification and covert colour-letter congruity effects if the two processes might rely on different areas, and second, it seems likely from recent structural MRI

data (James et al., 2003) that the parietal letter-activated area (see e.g., Price et al., 2003) is spared in D.F.

In conclusion, we have found no evidence from a series of studies for any covert perceptual processing of form that can influence D.F.'s behaviour when she is performing an overtly colour-related task. That is, when her task is to attend to colour, we can detect no sign of residual form processing in her perceptual system. However, when she is given tasks that require her to attend explicitly to form rather than colour, it becomes possible to detect signs of form processing, albeit only with the assistance of (presumed) downstream modulation derived from semantic representations of colour names. We did not find an analogous colour-congruity advantage in our shape-search task. One interpretation of this is that only colour-form associations in long-term memory have a facilitatory effect rather than colour cues per se, although an alternative explanation in terms of a working-memory deficit is possible. It may, however, be more likely that D.F.'s damage to LO has spared certain letter-specific processes and that these processes, although usually operating at a subthreshold level in her perceptual system, can have a significant effect upon her behaviour given explicit attention to letter-form and top–down modulation by colour cues.

Acknowledgements

References

Aglioti, S., Bricolo, E., Cantagallo, A., & Berlucchi, G. (1999). Unconscious letter discrimination is enhanced by association with conscious color perception in visual form agnosia. *Current Biology*, *9*, 1419–1422.

Berlucchi, G. (2003). Some effects of cortical and callosal damage on conscious and unconscious processing of visual information and other sensory inputs. *Progress in Brain Research*, *144*, 79–93.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., & Seitz, R. J. et al., (1998). Human anterior intraparietal area subserves prehension. A combined lesion and functional MRI activation study. *Neurology*, *50*, 1253–1259.

Culham, J. C., Danckert, S. L., Desouza, J. F. X., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually-guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, *153*, 180–198.

Dijkerman, H. C., & Milner, A. D. (1997). Copying without perceiving: Motor imagery in visual form agnosia. *NeuroReport*, *8*, 729–732.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*, 154–156.

Goodale, M. A., Meenan, J. P., Bülthoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, *4*, 604–610.

Goodale, M. A., & Milner, A. D. (2004). *Sight unseen*: *Explorations in conscious and unconscious vision*. Oxford: Oxford University Press.

Humphrey, G. K., Goodale, M. A., Jakobson, L. S., & Servos, P. (1994). The role of surface information in object recognition: Studies of a visual form agnosic and normal subjects. *Perception*, *23*, 1457–1481.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: A fMRI study. *Brain*, *126*, 2463–2475.

Joseph, J. E., Gathers, A. D., & Piper, G. A. (2003). Shared and dissociated cortical regions for object and letter processing. *Cognitive Brain Research*, *17*, 56–67.

Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience*, *20*, 3310–3318.

Macleod, C. M. (1991). Half a century of research on the Stroop effect—An integrative review. *Psychological Bulletin*, *109*, 163–203.

Malach, R., Reppas, J. B., Benson, R. B., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Science of the United States of America, 92*, 8135–8138.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.

Milner, A. D., & Heywood, C. A. (1989). A disorder of lightness discrimination in a case of visual form agnosia. *Cortex*, *25*, 489–494.

Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., & Heeley, D. W. et al., (1991). Perception and action in 'visual form agnosia'. *Brain*, *114*, 405–428.

Murphy, K. J., Racicot, C. I., & Goodale, M. A. (1996). The use of visuomotor cues as a strategy for making perceptual judgments in a patient with visual form agnosia. *Neuropsychology*, *10*, 396–401.

Polk, T. A. & Farah, M. J. (1998). The neural development and organization of letter recognition: Evidence from functional neuroimaging, computational modeling, and behavioral studies. *Proceedings of the National Academy of Science of the United States of America, 95*, 847–852.

Polk, T. A., Stallcup, M., Aguirre, G. K., Alsop, D., D'Esposito, M., Detre, J. A., & Farah, M. J. (2002). Neural specialization for letter recognition. *Journal of Cognitive Neuroscience*, *14*, 145–159.

Price, C. J., Gorno-Tempini, M. L., Graham, K. S., Biggio, N., Mechelli, A., Patterson, K., & Noppeney, U. (2003). Normal and pathological reading: Converging data from lesion and imaging studies. *NeuroImage*, *20*(Suppl. 1), S30–S41.

Tanaka, K. (1997). Mechanisms of visual object recognition: Monkey and human studies. *Current Opinion in Neurobiology*, *7*, 523–529.

Tootell, R. B. H., Tsao, D., & Vanduffel, W. (2003). Neuroimaging weighs in: Humans meet macaques in "primate" visual cortex. *Journal of Neuroscience*, *23*, 3981–3989.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.