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RESEARCH ARTICLE

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Monocular and binocular distance cues: insights from visual form agnosia I (of III)

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Abstract The human nervous system constructs a Euclidean representation of near (personal) space by combining multiple sources of information (cues). We investigated the cues used for the representation of personal space in a patient with visual form agnosia (DF). Our results indicated that DF relies predominantly on binocular vergence information when determining the distance of a target despite the presence of other (retinal) cues. Notably, DF was able to construct an Euclidean representation of personal space from vergence alone. This finding supports previous assertions that vergence provides the nervous system with veridical information for the construction of personal space. The results from the current study, together with those of others, suggest that: (i) the ventral stream is responsible for extracting depth and distance information from "monocular" retinal cues (i.e. from shading, texture, perspective) and (ii) the dorsal stream has access to binocular information (from horizontal image disparities and vergence). These results also indicate that DF was not able to use size information to gauge target distance, suggesting that intact temporal cortex is necessary for "learned size" to influence distance processing. Our findings further suggest that in neurologically intact humans, object information extracted in the ventral pathway is combined with the products of dorsal stream processing for guiding prehension. Finally, we studied the "size-distance paradox" in visual form agnosia in order to explore the cognitive use of size information. The results of this experiment were consistent with a previous suggestion that the paradox is a cognitive phenomenon.

Keywords Prehension · Binocular · Vergence · Distance cues · Visual form Agnosia · Human

Introduction

How do humans judge egocentric distance? The information used for gauging target distance has attracted scientific interest for well over a century but Cutting (1997, p. 69) has pointed out that the result of this interest is "little more than a plenum of lists". Cutting is referring here to lists of potential distance cues, including accommodation, aerial perspective, binocular disparity, vergence angle, height in the visual field, motion parallax, perspective and so on. It is only recently that the issue of *how* the human nervous system uses these various sources of information has been addressed. As a useful starting point, Cutting (1997) has provided a division of egocentric space into three regions: personal space (<1.5 m), action space (<30 m) and vista space (>30 m). Personal space has been established as being approximately Euclidean in nature, with action and vista space having an "affine" character, although increasing the amount of available information decreases the affine nature of action space (Cutting 1997). This observation raises the question of which cues can provide the distance information required for an Euclidean representation of personal space.

The purpose of the current study was to investigate distance processing in a patient with visual form agnosia in an attempt to gain an insight into how the nervous system uses cues to distance. Our interest arose in part from previous reports suggesting that patients with visual form agnosia predominantly use binocular information to scale their grasp aperture in a manual prehension task when reach distance is varied (Marotta et al. 1997). Marotta et al. (1997) showed that two patients with visual form agnosia failed to scale their grasp aperture appro-

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priately when viewing under monocular conditions; the patients had a wider maximum grip aperture when an object of constant size was closer to them and vice versa. Marotta et al. suggested that the failure to scale grip aperture occurred because the patients were unable to compute the distance of the target object monocularly and were thus unable to compute object size (perceived size is known to be a function of perceived distance; Emmert 1881). Contrary to this explanation, however, it has been found that patient DF (one of the two tested by Marotta et al. 1997) is able accurately to compute distance even when viewing monocularly (Carey et al. 1998; Mon-Williams et al. 2001). Marotta et al. described this aspect of their results as "paradoxical", but we suggest that the paradox may disappear if *depth* and *distance* processing are considered separately. In the perceptual literature, it is customary to reserve the term "distance" for egocentric judgements whilst the term depth is used to describe an object's dimension along the line of sight. If we use this terminology, Marotta et al.'s results suggest good distance processing but poor depth processing (the patients were required to grasp the object in the sagittal plane). In support of this interpretation, Dijkerman et al. (1996, 1999) demonstrated that patient DF could make good adjustments of hand orientation when reaching to grasp a target oriented in depth under binocular conditions, although with monocular viewing this was not possible (unless motion parallax cues were available). Nonetheless, the patient was well able to locate the target with her hand with normal accuracy under either viewing condition. We suggest, therefore, that patients with visual form agnosia are able to process disparity information about depth relatively normally for the purpose of visuo-motor control (we consider this further within the Discussion) but that the cues they use when judging distance remain to be resolved. We were interested particularly in the possible use of vergence and size cues in distance processing for reasons we will outline below. It should be noted that we will describe cues that are available with monocular viewing (such as texture, perspective) as "monocular" but this does not imply that this information is not available with binocular viewing.

Some recent studies have explored the use of binocular vergence in distance processing (Mon-Williams and Tresilian 1999a; Tresilian et al. 1999). The results of these studies have indicated that binocular vergence is a valuable source of egocentric distance information. This finding is somewhat at odds with the widely held view that vergence is unlikely to provide useful information in full cue environments (e.g. Brenner and van Damme 1998, p. 493). One reason for the lack of confidence in vergence as a distance cue is the fact that distance judgements show a "specific distance tendency" when vergence is the only cue; near objects appear further than their physical location whilst more distant objects appear closer. It has been argued, however, that this phenomenon is due to a general contraction bias occurring when observers are asked to make a range of judgements in conditions of uncertainty (see Mon-Williams and Tresilian 1999a; Tresilian et al. 1999). Instead, Tresilian et al. (1999) have argued that vergence provides a veridical source of information that is combined with other available cues according to a weighted averaging scheme. In this scheme, the significance (weight) accorded to vergence information decreases with: (i) increasing discrepancy between vergence information and other cues; (ii) reduced vergence demand (i.e. as fixation distance increases); (iii) the availability of other distance cues. According to this model, vergence plays a role as a distance cue in normal full cue viewing environments but the weighting attached to the vergence cue will be relatively low, even at close (25 cm) viewing distances. Given the reliance on binocular information for computing depth in patients with visual form agnosia (Dijkerman et al. 1996, 1999; Marotta et al. 1997), we were therefore interested in determining the weighting attached to vergence as a *distance* cue in patient DF.

Furthermore, we were interested in exploring the extent to which monocular and binocular cues interact in visual form agnosia. Tresilian and Mon-Williams (1999) have reported a remarkable illusion whereby egocentric target distance is judged to be significantly greater regardless of whether vergence angle is increased or decreased. The experiment of Tresilian and Mon-Williams involved participants pointing open-loop to targets within a small box (length of box=53 cm). Tresilian and Mon-Williams (1999) formulated a simple heuristic model to account for their finding of increased egocentric distance judgements. The model was based upon the premise that individuals use many sources of distance information to obtain a self-consistent representation of 3D space (see Brunswick 1952; Bruno and Cutting 1988). The heuristic model assumed that there were three interacting sources of information: the vergence angle of the eyes, horizontal disparities from the box-end and monocular cues providing information about box-end distance. They proposed that these cues interact as follows:

(a) The sensory estimate of convergence angle (γ') provided an estimate (D'_V) (the subscript v stands for vergence) of target distance (D) and interpupillary distance (I):

$$D'_V = I \cot \gamma', \tag{1}$$

(b) Relative horizontal disparity, R ($\approx dI/D^2$), provided information about the distance, d, between the target and the end of the viewing box. Combined with information about target distance and interpupillary distance I, disparity provided an estimate (d') of d,

$$d' = D'^2_V R/I = D'^2_V d/D^2 \tag{2}$$

Substituting for D'_V from (2):

$$d' = d[I \cot \gamma'/D]^2 \tag{3}$$

(c) Consistent (prism independent) monocular cues and vertical binocular disparities provided a reasonably accurate estimate of the distance of the box-end from the eye (E'). This information, combined with the disparity derived information about d (Equation 3), provided an estimate (D'_{ER}) (the subscript ER stands for end of box information together with relative horizontal disparity) of the target distance: $D'_{ER}=E'-d'$, hence:

$$D'_{ER} = E'\text{-}d[I \cot \gamma '/D]^2 \quad (4)$$

(d) The two sources of information about target distance provided by Equations (1) and (4) were combined by a weighted averaging process (Anderson 1981; Bruno and Cutting 1988; Massaro 1988) to give an overall estimate of target distance (D'_t) (the subscript t stands for total):

$$D'_t = w_1(D'_V) + w_2(D'_{ER}), \quad (5)$$

where w_1 and w_2 are weighting factors. Such a weighted averaging requires that the weights sum to one (e.g. Mulligan and Shaw 1980). Weights of this kind are often treated as factors which reflect the "confidence" that the nervous system attaches to different sources of information (e.g. Young 1971; see also Welch and Warren 1980; Massaro 1988). If the confidence associated with D'_V is c_1 and that associated with D'_{ER} is c_2 then the relative confidences, $c_1/(c_1+c_2)$ and $c_2/(c_1+c_2)$, sum to one and the weights (w_1, w_2) can be made equal to these. This scheme means that the weights are constrained to lie in the interval [0, 1]. The work of Marotta et al. (1997) and Dijkerman et al. (1996, 1999) strongly suggested that patients with visual form agnosia are insensitive to monocular information on depth. We decided, therefore, to study whether the heuristic model predicts the behaviour of a patient with visual form agnosia.

Another source of useful distance information is provided by the angle subtended by an object on the retina(e). If the size of an object is known then an object's angular size can provide information on the object's distance. Previous research has established that "learned size" cues play an important role in distance processing (Mon-Williams and Tresilian 1999c; Tresilian and Mon-Williams 1999). It is known that patients with visual form agnosia are unable to make cognitive judgements about object size (Milner et al. 1991), although they can use such information to guide their grasp (Goodale et al. 1991). We therefore decided to explore whether patient DF is able to use size cues as a guide to the distance of an object, in order to gain a better understanding of how information about size influences distance processing in the intact observer.

Finally, we decided to explore the "size-distance paradox" in visual form agnosia. The reason for running this study was that the size-distance paradox offers the opportunity of exploring the cognitive use of size information. Jeannerod (1988, 1994) proposed the term "semantic" for the use of information that relies upon object recognition (object constancy) in contrast to the "pragmatic" use of size information in modifying grasp aperture. This distinction maps onto the dissociation between perceptual judgements and vision for action (Milner and Goodale 1995), where perceptual judgements are associated with processing along the ventral occipitotemporal route and vision for action is processed via the dorsal pathway. When viewing similar targets that subtend the same visual angle at two different distances in reduced cue environments, observers report that the closer target is smaller and further away than the farther target, which is perceived to be larger and closer (e.g. Ono et al. 1974). This phenomenon has been referred to as the "size-distance paradox" (Ono et al. 1974). Mon-Williams and Tresilian (1999b) suggested that the size-distance paradox occurs because the distance percept is not cognitively penetrable and thus the apparent size of the target is used as a basis for verbal judgements of target distance. In other words, participants report that the target is further when its apparent size is smaller and vice versa, even though the apparent size arises from veridical (but not cognitively penetrable) judgements of target distance. Mon-Williams and Tresilian reasoned that apparent size is used as it is: (i) the most salient information when viewing a target in the complete absence of contextual cues, (ii) easy to remember and (iii) the easiest information to compare between subsequent stimulus presentations. It is possible to test this hypothesis in a patient with visual form agnosia. Patients with visual form agnosia are unable to make explicit verbal (Milner et al. 1991) or manual (Goodale et al. 1991) judgements about object size but can use size in a pragmatic fashion for pre-shaping grip. This means that a patient with visual form agnosia should make random forced choice judgements of target size and distance in the size-distance paradox paradigm. If asked to make simultaneous judgements of distance and size, however, the judgements should be random but correlated (i.e. smaller and further; larger and closer).

These ideas were tested in a series of experiments. The basic experimental design utilised a perturbation technique where vergence angle is altered without changing actual target distance. The technique involves the brief introduction of a prism over one eye: this manipulation changes the binocular parallax of a visual target and so changes the vergence demand. A prism orientated with its base nasal (in) will increase vergence specified distance whilst a prism orientated with its base temporal (out) will decrease vergence specified distance. Perturbing the vergence cue in this manner leaves all other cues to distance unaffected (see Tresilian et al. 1999; Mon-Williams and Tresilian 1999a).

Materials and methods

Patient DF

DF experienced carbon monoxide poisoning in 1988 with subsequent structural MRI scanning revealing a dense bilateral lesion in lateral pre-striate cortex. DF was 45 years old at the time of the current experiment. A detailed report of the presenting features of DF's case is provided elsewhere (Milner et al. 1991). A preliminary study using functional MRI indicates that viewing drawings of familiar objects causes little or no activation in occipito-temporal lobe structures in DF, strongly indicating a disconnection of these areas from primary visual cortex (James and Goodale, personal communication). A comprehensive eye examination at the time of the current experiment revealed an absolute inferior field hemianopia (Henson VFA II) with some macular sparing in both eyes. DF was slightly presbyopic (add +1.25 DS) but was otherwise close to emmetropia (R. +0.25/–0.50×180; L. +0.25/–0.50×180) as assessed by an experienced retinoscopist. Ophthalmoscopy and tonometry revealed healthy eyes.

Apparatus

We used a specially designed viewing box in order to run the experiments (Tresilian and Mon-Williams 1999). The viewing box was rectangular (90 cm long by 20 cm wide by 20 cm high) and lined with patterned paper on the walls and floor (proving a rich texture gradient), had its far end open and contained some familiar objects (providing potential relative size and ordinal cues to distance). It should be noted that although this condition was relatively "rich" with visual cues, the available information was still somewhat reduced compared to normal viewing (e.g. motion parallax was minimised and the vertical disparity gradient was relatively small). Observers viewed targets (thin strips of metal) through an aperture in the front of the box (10×5 cm). A moulded plastic restraint mounted in front of the aperture provided some support for the head, completely occluded peripheral vision, allowed DF to position herself correctly with respect to the box and acted as a light shield. The head restraint had a binocular occluder, which meant that DF could position herself within the apparatus before viewing presented targets. The restraint ensured that head movements were minimised during performance of the pointing tasks. The angular field of view was further restricted by a pair of trial frames (diameter 3 cm) into which ophthalmic prisms could be placed. The experimental task was to position the unseen index finger of the right hand such that its tip was placed on the outside of the viewing box at the judged distance of the target. The task was thus one of open-loop pointing to the location of the target. DF was allowed to take as long as she wanted and make as many adjustments as required to ensure that she was happy with the judged position. Prior to running the actual experiment, DF was provided with a reasonable amount of practice with the open loop pointing task (ca. 3 points at each target location) and given feedback on end point accuracy. Following this practice session, DF pointed to each target binocularly five times. The data from this session (mean of five points for each target position) showed that DF was able to point accurately at each of the targets – the data were not statistically different from the "no prism" data reported for the actual experimental conditions (see Results). The mean positional pointing accuracy was measured for 1 s at a sampling rate of 86 Hz using an electromagnetic movement recording system (accurate to within 3 mm).

Experiment 1

Five target positions were used in the experiment: the targets were placed through slots in the viewing box at 17, 20, 25, 33.3, and 50 cm (±0.5 cm) from the observer's eyes. These target distances were chosen so that the step size between each target position corresponded to 1 Metre Angle (the Metre Angle is approximately equivalent to the reciprocal of distance).

The experiment was designed to study the effect on DF's pointing responses when vergence specified distance was manipulated with ophthalmic prisms. DF therefore viewed the targets with (i) no prism in place or (ii) through a 6Δ prism (1Δ=the angle whose tangent is 0.01) either placed with its base towards the nose ("base-in") or (iii) orientated temporally ("base-out"). DF pointed to each target five times when viewing through each orientation of the prism and five times without a prism (ie a total of 75 trials) with the order of presentation randomised. The experiment was run under two conditions. In the first condition, the target size at each distance was set so that its vertical angular subtense was always approximately 1.9 degrees at the observer's eye (there was some variation in the target's angular size but this was not correlated with distance). This arrangement meant that DF could not use size information as a cue to distance. It was arranged that the targets placed at different distances were different coloured strips of metal. This arrangement ensured that there was no conflict between size and other distance information: if the target were always the same appearance then the constant size might suggest that the distance had not changed and so conflict with other distance cues. In the second condition the same target was used in all trials. Previous research has indicated that providing such a size cue dramatically decreases the weighting attached to other sources of information (Mon-Williams and Tresilian 1999c; Tresilian and Mon-Williams 1999; Tresilian et al. 1999).

Experiment 2

The second experiment was identical to the first apart from an alteration in the viewing box. In the second experiment the lined paper and objects were removed from the box and a thin Perspex sheet was placed within the box (providing a visible "box-end"). The visible surfaces of the box were smooth and painted matt black except in the middle of the box where a thin (0.5 mm) sheet of white translucent Perspex was located, behind which a 60 W bulb was placed. The Perspex sheet was 53 cm (±0.5 cm) from the centres of rotation of the observer's eyes. The bulb produced a homogeneous illumination from the end of the box (approximately 250 lux) and provided a matt white screen against which targets could be easily seen. The same target positions and prisms were used as in the first experiment (although a different randomised order was used). The target size at each distance was set so that its vertical angular subtense was always approximately 1.9 degrees at the observer's eye (there was some variation in the target's angular size but this was not correlated with distance). This arrangement meant that DF could not use size information as a cue to distance in experiment two. The apparatus was designed in this manner to ensure that the experimental conditions were identical to those used in a previous experiment (Tresilian and Mon-Williams 1999). The Perspex sheet was placed within the box for reasons explained in the introduction.

Experiment 3

A slightly different arrangement was used to study the size-distance paradox in DF. In this experiment, the target was a piece of tubing (0.7 cm width×3 cm height) illuminated by a small red light emitting diode and the box was light sealed with the room lights switched off to ensure that nothing was visible apart from the target. The apparatus was designed in this manner to ensure that the experimental conditions were the same as those used in a previous experiment (Mon-Williams and Tresilian 1999b). The tubing created a reasonable sized target that was readily seen but did not illuminate the box (and thus provide additional distance information). The room lights came on between trials to ensure that DF did not dark adapt. The target was directly in line with the right eye at a distance of 40 cm (±0.5 cm). The target was viewed through a prism placed in front of the left eye with its base orientated towards or away from the nose. Prism orientated base inwards increases the vergence specified distance whilst prism oriented base outwards decreases the vergence specified distance. The power of the prism was 6Δ, resulting in a vergence specified distance of 33.5 cm when the prism was orientated base outwards and approximately 49.6 cm when the prism was base inwards.

Each trial consisted of DF viewing the target through the prism orientated with its base towards or away from the nose. In ten trials the prism was initially orientated with its base inwards and in another ten trials the prism was initially orientated with its base outwards. The initial orientation of the prism was randomised across trials. DF was asked to memorise the distance of the target on the first presentation and then viewed the target through the prism orientated in the opposite direction. In the first condition, the experimental task was to make a forced choice verbal judgement on whether the target "*looks* closer or further than the preceding trial" (Ono et al. 1974; Mon-Williams and Tresilian 1999b). In the second condition the experimental task was to make a forced choice verbal judgement on whether the target "looks bigger or smaller than the preceding trial". In the third condition, the experimental task was to make a forced choice verbal judgement on whether the target "looks bigger or smaller than the preceding trial" *and* whether the target "looks closer or further than the preceding trial".

Results

Experiment 1

The results from the two conditions in the first experiment were almost identical. A *t*-test showed that the data from the two conditions were not reliably different. In other words, the addition of a size cue had no influence on DF's pointing responses, whether or not a prism was present. The relationship between the responses from conditions 1 and 2 was described by the linear relationship, y=0.99x+0.6 cm with an r^2=0.99, where y is the response from the first condition and x is the response from the second condition. Figure 1 (upper) illustrates the mean pointing response found in the two conditions. It may be seen that DF showed accurate pointing in the absence of the prism but that the prism had a large influence on her responses. This finding is very different from that found in normal observers; the middle plot of Fig. 1 shows typical data from neurologically intact observers (taken from Tresilian et al. 1999) where the prism causes a slight bias away from (prism orientated base nasal) or in from the target (base temporal). The remarkable conclusion from the first experiment is that DF seems to rely almost completely on vergence information to gauge target distance. This can be best appreciated from an inspection of the bottom graph in Fig. 1 where the mean reaching amplitude is plotted against the calculated vergence-specified distance of the target. Vergence-specified distance (D_v) was calculated in the following manner: let the vergence demand of the target without prism be γ_1 and vergence demand of the target with prism be γ_2 and Δ the prismatic displacement. Then, if the prism *increases* vergence demand, $\gamma_2=\gamma_1+\arctan\Delta$. The vergence specified distance, can be calculated as:

$$D_v = I\cot\gamma_2 \qquad (6)$$

where I is the interpupillary distance. It can be seen from the lower plot of Fig. 1 that 98% of the variance of DF's responses could be predicted from the vergence specified distance, despite the fact that there were a plethora of other distance cues (e.g. perspective, texture) present within the viewing environment (including size in condition 2). Notably, DF reported that it was "impossible to reach that far" when she viewed the 50 cm target through the base-in prism (where the vergence specified distance was 97.6 cm). Accordingly the data from this target configuration were not included in the analysis. These findings are in stark contrast to the normal influence of prisms on open-loop pointing in relatively rich cue environments

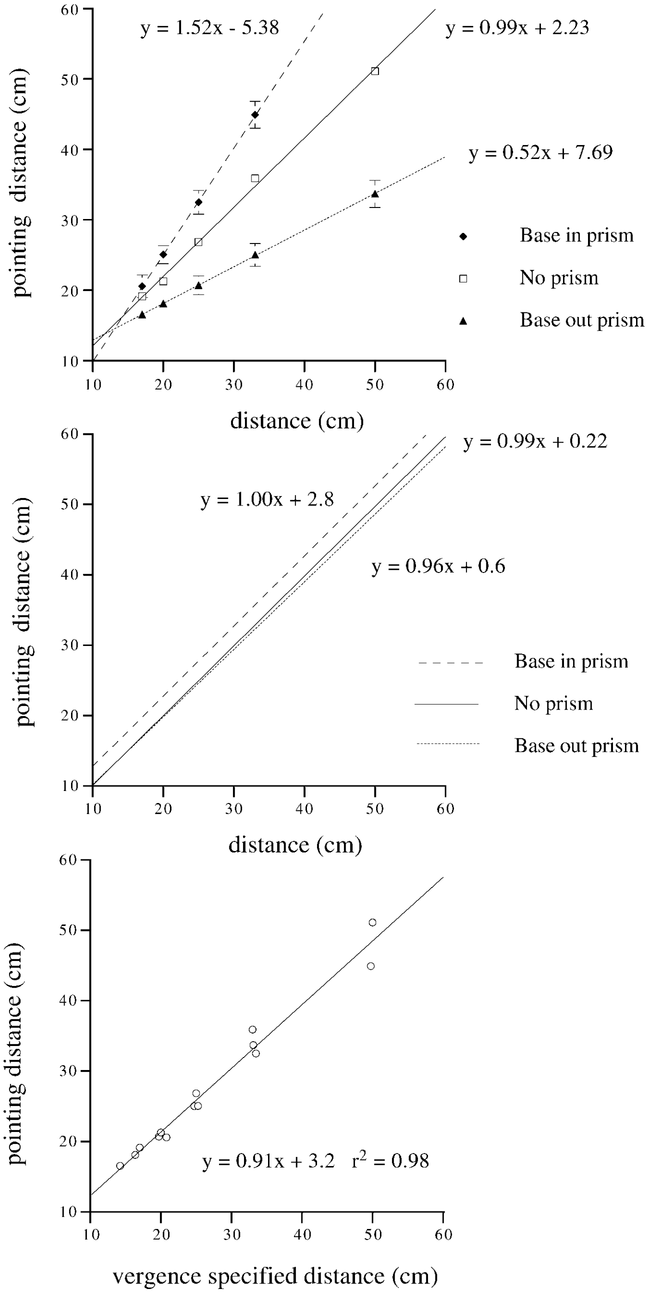

Fig. 1 *Upper panel*, pointing amplitude data from experiment 1 averaged across ten responses by DF (five from condition 1 and five from condition 2) plotted as a function of target distance. The *solid line* shows the response when no prism was in place, the *dotted line* shows the pointing response when viewing through a base-out prism and the *dashed line* shows the pointing response when viewing through a base-in prism. Standard deviation bars are shown except when smaller than symbol size. *Middle panel*, typical functions showing pointing distance plotted as a function of target distance in neurologically intact observers (taken from Tresilian et al. 1999) showing that the prism normally causes only a slight bias away from (base in, *dashed line*) or in from (base out, *dotted line*) the target. *Lower panel*, pointing data from DF plotted as a function of vergence-specified distance. It can be seen that the judged distance of the target is predominantly predicted by the vergence-specified distance (98% of the variance accounted for)

(see Tresilian et al. 1999). Moreover, the addition of size information normally diminishes the prismatic influence on perceived distance (Mon-Williams and Tresilian 1999c; Tresilian and Mon-Williams 1999; Tresilian et al. 1999).

An alternative way of thinking about the contribution of vergence to distance processing is to consider the weight attached to vergence (where the weight represents the "confidence" attached by the nervous system to a particular cue). Landy et al. (1995) have developed a definition for an empirical measure of cue weight based on a weighted averaging model. The measure relies on changing one cue whilst holding several others constant. For distance processing, the weight is the change in judged distance expressed as a proportion of the change in a given cue (prism induced vergence discrepancy in the current experiment). The change is the difference between the judged distance of a target with vergence discrepant and with vergence concordant (no prism). Thus, the ratio (pointing distance difference)/(vergence discrepancy) is an empirical measure of vergence weighting conforming to Landy et al.'s (1995) definition. Tresilian et al. (1999) named this measure the "prism bias ratio" (PBR). The PBR can be calculated as follows: for each target position, the pointing distance when viewing through the prism is subtracted from the pointing distance when viewing without the prism. This difference is then divided by the difference between the target's physical distance and the vergence specified target distance with the prism in place. Analysing DF's pointing data in this fashion produced two interesting results. First, the analysis suggested that there was no relationship between target distance and the weight attached to vergence (as measured by the PBR). In normal participants the weighting attached to vergence decreases as fixation distance increases but this relationship was not present in DF ($r^2<0.1$ for both the base-in and the base-out prism). Second, a difference was found between the PBR measured when the prism was orientated base-in and base-out. The mean PBR was equal to one when the prism was orientated base-out (ie the maximum possible weight was attached to vergence). In contrast, the mean PBR was 0.67 when the prism was orientated base-in. The difference in PBR between conditions was statistically reliable [$t(3)=3.89$, $P<0.05$]. This result is consistent with previous reports (Tresilian and Mon-Williams 2000) of the nervous system decreasing the weight attached to vergence information when that conflicts with other available cues by indicating a further distance than those other cues. Tresilian and Mon-Williams (2000) suggested that the difference in weighting arises because of the decreased reliability associated with increasing fixation distance. This analysis therefore suggests that "monocular" retinal information can influence distance processing in visual form agnosia, but that the weighting attached to this information is extremely low and generally swamped by the vergence contribution. The exception appears to occur only when vergence indicates a "further" distance than all other available information. In this situation, the cue discrepancy seems to lower the weight attached to vergence and increase the confidence attached to other cues. Further support for the use of monocular information in DF comes from the variability of the pointing response. Inspection of Fig. 1 (upper) shows that the pointing was less variable when there was no conflict between vergence and the other cues (ie in the no prism trials). This suggests that the monocular cues were contributing to the final pointing response, although their contribution becomes reduced as soon as they conflict with the vergence signal. It should also be noted that the response variability becomes larger as fixation distance increases. This finding can be explained with regard to the higher noise associated with the vergence signal as fixation distance increases (see Tresilian et al. 1999). An alternative explanation suggested by an anonymous reviewer is that the greater variability is due to the increase in neural noise associated with a movement of greater magnitude. A previous study conducted by Tresilian et al. (1999) suggests that the increased variability is more likely to be due with the noise associated with the distance information rather than the motor signal. Tresilian et al. showed that variability remains constant when pointing at targets located between 25 cm and 100 cm in full cue conditions but demonstrated that the variability increases when pointing in situations where vergence is the only distance cue. The second experiment was run in order to explore further the use of monocular distance cues in visual form agnosia.

Experiment 2

Figure 2 shows the results from the second experiment. It can be seen that the presence of the box-end had no effect on the no-prism results and little effect on the base-in responses. In contrast, the box-end caused a large change in the pointing responses made when viewing through the base-out prism. The change in pointing response is predicted from the heuristic model outlined in the introduction (Tresilian and Mon-Williams 1999) and provides evidence that although DF relies primarily on binocular distance cues she is sensitive to some monocular information. The results also provide additional support for the findings of Marotta et al. (1997) and Dijkerman et al. (1996, 1999) showing that DF can use binocular disparities to estimate depth intervals. Nonetheless, the effect of the box-end is far less than that found in participants without visual form agnosia – viewing through a base-out prism normally results in participants over-pointing in these viewing conditions (Tresilian and Mon-Williams 1999). The results of the second experiment support the idea that DF relies predominantly on binocular cues in distance processing but that monocular cues can make a small contribution, especially under certain viewing conditions. The results from the first two experiments suggest that monocular distance cues are predominantly processed in the ventral stream but also indicate that patient DF has some access to such cues. It is not clear how monocular cues can in-

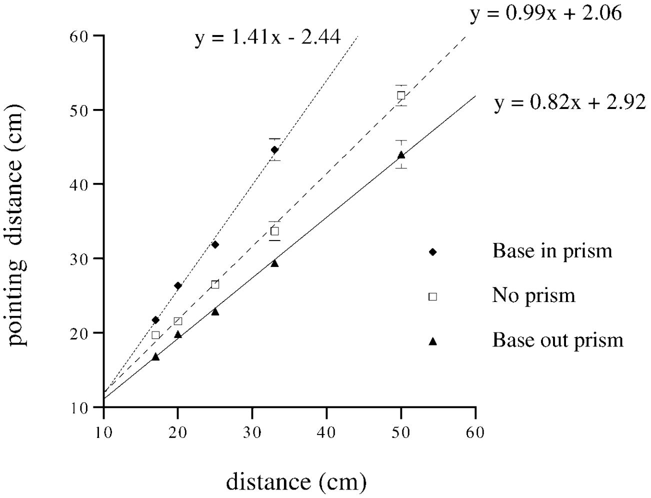

Fig. 2 Pointing amplitude data from experiment two averaged across five responses by DF plotted as a function of target distance. Standard deviation bars are shown except when smaller than symbol size. Comparison of the slopes and biases for the respective conditions shown in Fig. 1 (upper panel) demonstrates that the presence of the box-end had an effect on DF's pointing response

fluence DF's distance perception, but there are various possibilities. First, it is possible that the ventral stream is not *completely* disconnected from primary visual cortex in DF. Second, it may be the case that some early processing of monocular cues to depth and distance occurs in primary visual cortex. Third, it is possible that a limited amount of depth/distance processing occurs within the dorsal stream. We are not able to differentiate between these different possibilities.

Experiment 3

The results from the third experiment (size-distance paradox) were clear cut. In condition 1, DF's responses were at chance when asked to judge whether the target was smaller or bigger than the previous presentation (50% of the responses were predicted by prism orientation). In condition 2, DF's responses were still at chance when asked to judge whether the target was closer or further (60% of the responses predicted by prism orientation). In the third condition, her responses were still at chance when asked to judge whether the target was closer or further *and* whether it was bigger or smaller (55% of the responses predicted by prism orientation) but the two judgments always agreed perfectly (i.e. she always reported bigger and closer *or* smaller and further).

Discussion

The results indicate that patient DF relies predominantly on a signal from vergence effort to gauge the distance of targets in personal space. Indeed, under the experimental conditions we used, pointing amplitude was well predicted by vergence specified distance. The results of experiments 1 and 2 provide evidence that DF has some degree of sensitivity to "monocular" distance cues but that she attaches little confidence to this information. One might expect, therefore, that preventing DF from using vergence cues by having her close one eye would seriously reduce the accuracy of her reaching. In fact, Marotta et al. (1997) and Carey et al. (1998) have shown that DF can reach accurately even under monocular viewing conditions. It is worth considering, therefore, what information was missing from the current experimental apparatus that DF might have been able to use in these other experiments. Vertical retinal image disparities have the potential to provide information on the distance of a fixated target (Mayhew and Longuet-Higgins 1982). It has been established, however, that a wide (>30°) viewing angle is required for the nervous system to exploit this distance cue (Bradshaw et al. 1996). The viewing angle was considerably reduced within the viewing box making it unlikely that DF would be able to use this cue (although DF may have learned to be more sensitive to this cue than individuals without visual form agnosia). The issue of whether DF can use this information in normal viewing conditions therefore remains unresolved; but in any case vertical disparity cues would not have been available to her in monocular viewing conditions.

The other important distance cue missing from the current display was "vertical gaze angle" (the targets were all presented at eye height). In normal conditions, there is a fixed relationship between the distance of a target and the angle subtended between the eye and the ground plane (the "ground plane" refers to any flat horizontal surface such as a table top). We have data showing that DF uses this information in a prehension task when available (Mon-Williams et al. 2001) and that this information is used in the intact nervous system (Gardner and Mon-Williams 2001). In the tasks of Marotta et al. (1997) and Carey et al. (1998), as in all other previous tests of prehension in DF, the cue of vertical gaze angle would have been available, and would presumably therefore have been used under monocular test conditions to ensure accurate reaching. Although this cue was not available in our task, there were of course a number of other monocular cues to distance present in DF's visual field (e.g. perspective, texture). The data, however, clearly show that DF relied predominantly on a signal from vergence.

In the second condition (where the same target was used for all trials), DF seemed unable to use a size cue to determine target distance. This finding is in stark contrast to normal performance, where the provision of a size cue causes a large decrease in the weight attached to other distance cues (Mon-Williams and Tresilian 1999c; Tresilian and Mon-Williams 1999; Tresilian et al. 1999). DF has a lesion de-afferenting the object-recognition systems in inferior temporal cortex (James and Goodale, unpublished data). It seems reasonable to suggest that DF is unable to match a given object across successive presentations, thus making it impossible for her to use the angular size of an object as a distance cue.

In our experiment examining the size-distance paradox, DF showed no ability to judge either the size or distance of the presented target with respect to the previous trial. This result is consistent with previous reports that DF is unable reliably to retain visual information about size (Goodale et al. 1994) or location (Milner et al. 1999) even over a few seconds. Notably, however, her responses were completely consistent when she was asked to make simultaneous judgements regarding the size and distance of the target (i.e. she either reported smaller and further *or* bigger and closer). Mon-Williams and Tresilian (1999b) argued that the size-distance paradox arises because the distance percept is cognitively impenetrable and thus observers rely on apparent size when making verbal reports of apparent distance (i.e. the observers reason that if the target looks smaller then it must be further and vice versa). It is clear that DF can neither memorise the size nor the distance but carried out similar reasoning (either implicitly or explicitly); if reporting that it was smaller she reasoned that the appropriate companion response was that the target was further and vice versa. These results thus provide support for the notion that the size-distance paradox is a cognitive phenomenon and one which DF exhibits despite the loss of reliable visual inputs into her cognitive processing system.

Conclusions

These results have clear implications for the use of vergence information in normal distance processing. It has long been recognised that vergence contributes to the processing of an object's distance in reduced cue environments. Nonetheless, near objects are known to appear a little further away than their physical location whilst distant objects appear closer when their distance is specified by vergence information alone. Thus, participants' distance estimates (D) are directly proportional to the actual distance:

$$\hat{D} = mD + c, \quad 0.4 < m < 1, \quad c > 0 \qquad (7)$$

where m and c are constants for a particular individual performing a particular distance estimation task. The line described by Equation (7) will cross the $\hat{D} = D$ line at some point (D_s). Thus, Equation (7) suggests a contraction of perceived space around the point D_s with points closer than D_s to the observer appearing further away (tending towards D_s) and points further away than D_s appearing closer (again tending towards D_s). This kind of observation led Gogel (1969; Gogel and Sturm 1971) to refer to observations described by a relationship such as Equation (7) as displaying a "specific distance tendency" (SDT) where D_s is the specific distance to which other distances tend. The presence of the SDT has been used to argue that vergence is unlikely to be used as a distance cue in full-cue environments. In contrast, Tresilian and Mon-Williams (Mon-Williams and Tresilian 1999a; Tresilian et al. 1999) have argued that the SDT is an example of what Poulton (1989, p. 178–181) named a "contraction bias": a general tendency to bias responses towards the centre of the range of possible responses in an experiment. Tresilian and Mon-Williams further suggested that such biases only have significant effects under conditions of uncertainty. When there is insufficient information to be confident of where the target actually is, a contraction bias will tend to maximise the average accuracy of responses. Thus, the more uncertain the experimental conditions then the bigger the effect of the contraction bias. In support of this idea, Tresilian et al. (1999) systematically removed information from a viewing environment and showed that the contraction bias increased as the informational content of the display decreased. Tresilian et al. (1999) suggested that vergence does supply veridical information and provided evidence that this cue is used within a weighted averaging scheme for the determination of target distance. The data from DF show that vergence can allow for a geometrically veridical representation of personal space and thus the data support the conclusions of Tresilian et al. (1999).

The current data are also informative with regard to distance and depth processing in visual form agnosia. In many respects, our conclusions are similar to those of Marotta et al. (1997). In common with Marotta et al., we find that binocular cues are of particular importance for patients with visual form agnosia, and therefore (by inference) in the normal operation of the dorsal stream. In Marotta et al.'s experiment, DF was able to move her hand to the correct distance when reaching to grasp an object under monocular viewing but she could not scale her grasp aperture to an object's size consistently across different distances. We suggest, however, that Marotta et al.'s findings tell us more about DF's processing of depth rather than her processing of distance information (see Introduction). Marotta et al. suggested that the failure of grasp scaling was due to an inability to gauge distance (as the size of an object is computed as a function of its apparent distance). This explanation conflicts with their own data (as they acknowledge). An alternative explanation (consistent with all the data) is that DF was able to use vertical gaze angle information to gauge target distance with good accuracy under monocular viewing (Mon-Williams et al. 2001). The accurate distance information would allow DF to gauge the size of the object in the fronto-parallel plane: and indeed we know from other experiments that DF has no problem in scaling her grip in this plane for objects at different distances under monocular viewing (manuscript in preparation). In order to gauge the depth of the object, however, DF would need to recover information about the object's three-dimensional structure. One source of depth information is available from horizontal retinal image disparities and Marotta et al.'s (1997) data suggest that DF can use this depth cue (which can be gleaned either through binocular viewing or through motion parallax: Dijkerman et al. 1996, 1999). In the absence of binocular vision, it is necessary to recover depth from "monocular" retinal information (contours, texture, shading etc.). It is clear that neurologically intact humans are extremely proficient at extracting depth from the monocular retinal image. The fact that DF cannot recover depth when viewing monocularly suggests that an intact occipito-temporal processing pathway is necessary for extracting depth from shading, texture, perspective etc.

Landy et al. (1995) have suggested that normal depth and distance processing involves the integration of multiple cues, so that information from a wide range of sources is combined in some kind of weighted averaging scheme (where the weights attached to the various cues are equal to one). DF can be regarded, to a first approximation, as functioning with an isolated dorsal stream, which is not privy to many of the monocular cues available to an intact visual system. It seems reasonable to suggest that horizontal disparities constitute the primary information available to her for recovering object *depth*, so that for her this cue has a high weighting attached to it. In normal observers, the removal of the disparity cue will mean that the weight attached to other information (eg shading, texture and perspective) will increase and thus allow the system the best possible estimate of depth from the available data. It can be readily demonstrated that adult humans can use monocular cues to carry out a visuomotor task. It follows, therefore, that the information carried by the ventral and dorsal stream must ultimately be combined at some stage (in observers with intact visual processing) in order for the system to take advantage of the multiple cues carried in each stream.

A similar argument can be made with regard to *distance* processing. Normal observers use a wide range of information including vergence angle, texture, perspective, shading etc. and attach a weight to each cue to provide the best estimate of distance. The current data strongly suggest that DF finds it difficult to exploit the monocular retinal cues to distance. This means that DF must rely predominantly on vergence angle, vertical gaze angle and possibly vertical disparities when judging a target's distance. The removal of one of these cues means that the weight attached to the other(s) will increase but still allow DF to make judgements on target distance. In the current experiments, the absence of vertical gaze angle information and the lack of a sizeable vertical disparity gradient means that the vergence distance cue had the maximum weighting attached to it (or at least that the weighting attached to the "monocular" cues was extremely low). Nonetheless, it is not possible to draw conclusions about the relative weighting attached to cues in normal distance processing from these observations. The extent to which the system "prefers" one cue over another in normal distance processing is an empirical issue that needs to be resolved by determining the weighting attached to the various cues (see Landy et al. 1995; Tresilian et al. 1999).

The current study sheds some light on the possible organisation of the dorsal and ventral steam (as we know that DF has a damaged ventral stream but probably an intact dorsal pathway). First, it can be concluded that the ventral stream is responsible for extracting depth and distance information from the "monocular" retinal image (e.g. from shading, texture, and perspective). Second, the fact that DF can recover depth when viewing binocularly suggests that information regarding depth from disparity is available to the dorsal stream. Third, the absence of monocular depth and distance cues in the dorsal stream suggests that the "pragmatic" retinal size information carried by the dorsal stream is largely two dimensional, allowing DF to scale her grip aperture with monocular viewing when grasping an object in the fronto-parallel plane but not the sagittal plane. Finally, if we accept that the various cues are combined to compute depth and distance (and there is overwhelming empirical evidence that this is the case), the data from this study and that of Marotta et al. (1997) suggest that the brain must somehow combine information from the ventral stream regarding the surface and contextual properties of objects with the products of metric processing from within the dorsal stream.

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