RESEARCH ARTICLE

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The removal of binocular cues disrupts the calibration of grasping in patients with visual form agnosia

Abstract The present study tested the idea that the visuomotor systems mediating prehension do not have independent access to pictorial cues processed by perceptual mechanisms. Individuals with visual form agnosia, whose perceptual systems are compromised but who have intact visuomotor control, were examined to determine whether they could use pictorial scene cues to calibrate manual prehension when binocular information was removed. The removal of binocular cues produced considerable disruptions in size-constancy of grip aperture, which, combined with earlier observations in normal subjects, suggests that binocular cues are of primary importance in calibration of grasping. In the absence of binocular vision, normal subjects can use pictorial information, information that is severely compromised in individuals with visual form agnosia, to compute the distance (and thus the size) of the goal object. Thus, individuals with visual form agnosia must rely on a retinal image that remains uncalibrated, leading to inaccurate calibrations of grip aperture. The fact that these individuals scaled their grasp much less accurately under the monocular viewing condition, despite showing normal binocular grasping, suggests that pictorial cues to depth, which are presumably processed by mechanisms mediating our perception of objects and events in the world, can be accessed by visuomotor mechanisms only indirectly. These results, together with others, suggest that the visuomotor system 'prefers' to use binocular information and uses pictorial cues only as a last resort.

Key words Prehension · Monocular · Binocular · Visual agnosia · Pictorial cues

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Introduction

When we look at an object in the real world, it will inevitably appear larger than some objects and smaller than others in the same scene. The same is true with respect to its distance: the object will appear closer than some objects and more distant than others. Such comparisons are an obligatory part of the perceptual process. But relative judgements of this kind, while important for identifying objects and establishing the relationships between them, are not enough to calibrate or control any skilled movements that might be directed at those objects. If we attempt to pick up our coffee cup, for example, we must know more than the fact that the cup is further away (and smaller) than the book we are reading; our visuomotor system must compute the true size and distance of the cup and program our reach and grasp accordingly. Moreover, such computations must be carried out with respect to the frame(s) of reference most appropriate to the motor act that is to be performed (for example, retina- and head-centred coordinates for eye movements; head-, torso-, and perhaps shoulder-centred coordinates for reaching movements with the limb).

These differences in the requirements of visual perception and the visual control of action suggest that a single general-purpose representation of the world could not serve both functions. Instead, the different transformations required for perception and action would appear to require separate visual mechanisms, each adapted to the requirements of the output system it serves. Goodale and Milner (1992) have proposed that these two functions of vision can be mapped onto the two prominent cortical visual pathways that have been identified in the primate brain: a ventral stream of projections from primary visual cortex to the temporal lobe and a dorsal stream from primary visual cortex (and the superior colliculus via the pulvinar) to the posterior parietal cortex (Ungerleider and Mishkin 1982).

According to Goodale and Milner (1992), both streams process information about object features and about their spatial locations, but each stream uses this vi-

sual information in different ways. In the ventral stream, this information is transformed to deliver the enduring characteristics of objects and their relations, permitting the formation of long-term perceptual representations of the world. Such representations play an essential role in the identification of objects and enable us to classify objects and events, attach meaning and significance to them, and establish their causal relations. Such operations are essential for accumulating a knowledge-base about the world. In contrast, the transformations carried out by the dorsal stream deal with moment-to-moment information about the location and orientation of objects in egocentric coordinates and thereby mediate the visual control of skilled actions, such as manual prehension, directed at those objects.[1]

Even though the two systems work together in everyday life, under the right conditions it is possible to demonstrate a dissociation between perception and action in the normal observer. One condition in which this dissociation can be demonstrated is with figural displays where visual information is limited to static monocular cues. These cues are typically called *pictorial cues* because they are exploited by artists who use them to depict a three-dimensional world on a two-dimensional canvas. They do not lend themselves easily to formal classification but include such things as linear perspective, texture gradients, occlusion, familiar size, relative size, object shape, shading, and elevation in the visual field. Many of them, such as familiar size, probably depend heavily on learning. As we will see, these cues may play a more important role in perception than they do in the control of skilled actions.

In fact, with some pictorial displays our perception of object features such as size can be at odds with what our visuomotor system has computed. For example, Aglioti et al. (1995) recently demonstrated that the calibration of grip aperture during grasping is remarkably insensitive to the pictorial cues that drive the perception of familiar size-contrast illusions such as the Titchener Circles (or Ebbinghaus) illusion. Thus, even though subjects' perception of the relative size of two discs was affected by the background against which the discs were displayed, the scaling of their grip aperture (measured in flight) was largely determined by the true size of the target disc. Similar dissociations between visuomotor control and perceptual report have been observed with the horizontal-vertical illusion (Vishton and Cutting 1995), the Ponzo illusion (Brenner and Smeets 1996; I. Whishaw, personal communication), and the Müller-Lyer illusion (Gentilucci et al. 1996; but see Welch and Post 1996). Of course, the calibration of skilled motor outputs, such as grasping, is not entirely immune to the effects of pictorial illusions. Indeed, as we shall see, normal subjects can

use pictorial information to program and control their grasping movements – particularly in the absence of binocular information. Nevertheless, what is impressive is the fact that perceptual judgements are much more likely to be affected by pictorial illusions than are skilled motor outputs (for review see Goodale and Haffenden in press).

But why should the perception of object size be so susceptible to pictorial illusions of the kind just described while visuomotor control is not? As was argued above, perceptual mechanisms make use of the entire visual array; the relations between objects in the array play a crucial role in scene interpretation. Pictorial cues provide some of the most important information about the nature of objects and their relations in the scene. These pictorial cues can, if cleverly arranged, create the illusion that objects are bigger or smaller than they really are, often by providing incorrect information about the apparent relative distance of elements in the array (Coren and Girgus 1978; Gregory 1963). For perception, however, such illusions are of little consequence. In contrast, if the execution of a goal-directed act such as manual prehension, which must be calibrated with respect to the true metrics of the situation, falls prey to such illusions it will fail. As a consequence, systems which control tasks such as these are likely to ignore the available pictorial cues and make use of cues that are based entirely on the goal object itself. For example, the correct grip aperture during manual prehension can be reliably computed from the retinal image size of the goal object, if that image is properly calibrated with an accurate estimate of object distance.

One reliable source of distance information for the calibration of reaching and grasping is binocular vision. Servos et al. (1992) demonstrated that grasping movements made under monocular viewing were less 'efficient' than those performed under binocular viewing conditions, achieving lower peak velocities and showing prolonged periods of deceleration during the closing phase of the grasp. But even though this shows that binocular information plays a significant role in prehension, the subjects were still able to pick up the goal objects with little difficulty when binocular vision was denied, suggesting that the available monocular cues were sufficient to calibrate their grasp. One very reliable monocular cue is retinal motion, the motion of the object (and the scene) on the retina, particularly motion generated by movements of the head. Nevertheless, recent research by Marotta et al. (1995) found that subjects wearing an eye-patch did not try to increase the available retinal motion information by making larger head movements while reaching under monocular viewing. Individuals who had had an eye surgically removed for 1 year or more prior to testing did make use of this strategy, however. Taken together, these results suggest that the use of retinal motion cues for the control of prehension is a learned strategy and not one used spontaneously by subjects with normal vision.

So, the question remains as to which of the many available cues, or combination of cues, normal subjects use to calibrate accurate grasping under monocular view-

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[1] Note that when we use the term 'visual perception' we are using it in the sense of conscious visual experience – namely, in the sense of those visual processes that allow us to assign meaning and significance to external objects and events – even though we recognize that the term is sometimes used to refer to all the visual processing that occurs after light strikes the retina

ing conditions. One possibility is that subjects can learn to use pictorial information to help calibrate reaching movements. The familiar scene-based pictorial cues discussed earlier could theoretically provide depth and size information to these subjects when binocular information is removed. Other pictorial cues, such as occlusion and object shape, as well as information provided by texture gradients and shading, could also be used. The possible use of these cues has been a focus of research in our laboratory. Kruyer et al. (1996), for example, found that when most pictorial cues were removed by presenting 'glowing' spheres as targets for a grasping movement in the dark, subjects were quite impaired when performing monocularly. But while this result shows that pictorial cues make a contribution to the calibration and control of grasping, we know from a long history of work with pictorial illusions that such cues can be misleading. The visuomotor system would be better served by relying less on pictorial cues than on more reliable sources of information, such as that provided by binocular vision. In fact, in a recent series of studies in our laboratory (Marotta and Goodale 1996, 1997) we have shown that although subjects will use elevation of the target in the visual field to predict the amplitude and aperture of the required grasp, they will do this only when binocular information is not available. Moreover, as we have already seen in the work by Aglioti et al. (1995), subjects confronted with pictorial illusions under binocular viewing conditions will nevertheless calibrate their grasps appropriately. The misleading pictorial information affects their perceptual judgement, not their visuomotor control, suggesting that the pictorial cues are processed by perceptual mechanisms in the ventral stream of visual processing. This does not mean, of course, that the visuomotor systems in the dorsal stream do not have access to this information. Normally, however, these cues appear to be a supplemental rather than an integral part of the computations underlying manual prehension. We propose that the visuomotor systems in the dorsal stream gain access to these pictorial cues only via their links with the ventral stream mechanisms mediating perception of the scene. They have no direct access to this information from early visual areas.

While this proposal is consistent with the findings reviewed above, it has not been directly tested. The present study represents an attempt to evaluate this proposal by examining the behaviour of individuals with visual form agnosia – individuals whose perceptual systems are severely damaged but who have relatively intact visuomotor control of their grasping movements. The question we asked was as follows: Could these individuals, who are by definition unable to process form-based pictorial information in order to perceive an object, still use the available pictorial scene cues to help calibrate their reaching and grasping movements when normal binocular information was removed? If these patients have difficulty in calibrating their grasp under monocular viewing it would suggest that pictorial information may normally reach visuomotor control systems in the dorsal stream only via the ventral

stream mechanisms that mediate the experiential perception of visual scenes – networks which are presumed to be damaged in these visual agnosic patients.

The first patient we tested was DF, a young woman who had developed profound visual form agnosia following carbon monoxide poisoning. Even though DF's 'low-level' visual abilities are reasonably intact, she can no longer recognize even the simplest of geometric shapes. Nevertheless, despite her profound inability to perceive the size, shape and orientation of visual objects, DF can direct accurate and well-formed grasping movements, indistinguishable from those shown by normal subjects, towards the very same objects she cannot identify or discriminate (Goodale et al. 1991; Milner and Goodale 1993). What visual information is she using to calibrate these apparently normal grasping movements? It is possible, of course, that the intact visuomotor system mediating her prehension movements remains sensitive to a broad range of visual cues, including pictorial information, texture, shading, stereo, and retinal motion. The very fact that she can place her fingers correctly on the boundaries of the goal objects suggests that some of the visuomotor systems involved in mediating the grasp must be sensitive to information about the structure and orientation of the goal object. This does not necessarily mean, however, that her visuomotor system is able to use pictorial information derived from the arrangement of objects in the scene to compute the distance (and thus the size) of the goal object. It may instead use cues such as stereo and/or convergence which rely on the laws of physical optics rather than on convention and learning.

For these reasons, we compared the kinematics of DF's grasping movements to a goal object under normal binocular viewing and under monocular viewing. We anticipated that the removal of binocular information would disrupt DF's performance much more than control subjects who, of course, could fall back on pictorial scene cues to object distance. After testing DF, we had an opportunity to examine the performance of JW, another patient with visual form agnosia. Like DF, JW is also unable to recognize familiar three-dimensional objects or their line drawings.

Materials and methods

The experiment was carried out at the University of Western Ontario in compliance with the Social Sciences and Humanities Research Council (Canada) Guidelines (1981).

Subjects

Case description of DF

A profound visual form agnosia has already been well documented in this 39-year-old woman, who suffered an anoxic episode as a result of carbon monoxide poisoning in 1988. Detailed descriptions of her residual perceptual abilities are available elsewhere (Goodale et al. 1991; Milner et al. 1993). Magnetic resonance imaging revealed evidence of diffuse brain damage consistent with

the anoxia; the ventrolateral regions of her occipital lobe were particularly compromised, though primary visual cortex appeared to be largely spared. As mentioned earlier, DF shows accurate object-directed grasping, despite an inability to identify the object's form. These and other observations have led Goodale and Milner (1992) to propose that the damage in DF's cortical visual system is concentrated in the ventral stream of projections from primary visual cortex to temporal cortex, a set of pathways thought to be critical for the visual perception of objects. Her dorsal stream, projecting from primary visual cortex to the posterior parietal region, appears to be largely intact, allowing her to demonstrate good visual control of object-directed actions.A 39-year-old woman, LW, was tested as an age-, handedness- and sex-matched control for DF. Two more control subjects, KN (24 years old) and AH (23 years old), were used as additional sex-matched control subjects for DF. DF and her control subjects all have stereoscopic vision in the normal range with assessed stereoacuity of 40″ of arc or better as determined by the Randot Stereotest (Stereo Optical, Chicago). These subjects were strongly right-handed, as determined by a modified version of the Edinburgh Handedness Inventory (Oldfield 1971).

Case description of JW

JW is a 38-year-old, left-handed male who developed visual form agnosia following a major cardiac event which produced anoxic encephalopathy. Computed tomographic scans show evidence of multiple hypodensities in both occipital lobes, consistent with remote ischaemic infarction (probably thrombo-embolic). The final diagnosis was of generalized atrophy and ischaemic infarction in both occipital lobes, also extending into the right parietal region. The pattern of brain damage in JW is not identical to that seen in DF. Nevertheless, as we will see, the deficit he shows in object recognition and pattern perception in combination with a relatively spared visuomotor performance, at least in some domains, is similar to that observed in DF.

Visual fields and acuity. Goldman perimetry revealed a left upper quadrantanopsia, consistent with the lesion being more marked in the right hemisphere (Mapelli and Behrmann, in preparation).

Object recognition. JW is impaired at recognizing familiar objects, presented as real three-dimensional objects or as black-and-white line drawings. Nevertheless, he can provide rich and detailed definitions of them when given the auditory label for the object (Mapelli and Behrmann, in press and in preparation). The findings are all consistent with a recognition deficit restricted to the visual modality.JW is also profoundly impaired at face recognition, although he can make use of cues such as hair length and facial hair to make coarse judgements about gender. His ability to recognize letters is somewhat better than that for objects or faces, largely because this has been the focus of intensive therapy over the last year. In this respect, his visual abilities are somewhat better than DF's. As with other visual discriminations, however (see below), when he has to make fine perceptual judgements about visually confusable letters, performance declines markedly.

JW's profound impairment in object recognition arises from deficits in basic visual processing, rather than a deficit in visual/semantic association. For example, whereas he can differentiate between geometrical figures such as a square and a circle, he has difficulties making finer discriminations between a circle and an oval or a square and a rectangle. He is also unable to make reliably correct same/different judgements between rectangles which have different dimensions but are the same in overall area (Efron 1969). He shows abnormally slow, although reasonably accurate, performance on visual search tasks for targets defined by orientation (horizontal/vertical) or curvature (curved/straight). Again, in these kinds of tasks he does better than DF. But like DF, he performs much better on search tasks where the target is defined by colour. This latter finding is consistent with the preserved colour skills as manifested in his normal performance on the Farnsworth-Munsell test for colour discrimination. JW is also impaired at figure ground

discrimination, at judging the symmetry of shapes (Vecera and Behrmann, in press) and at performing simple visual image segmentation of overlapping shapes.

A 28-year-old male, RK, was tested as a sex- and handedness-matched control for JW. While JW had an assessed stereoacuity of 100″ of arc, RK had stereoscopic vision in the normal range with assessed stereoacuity of 40″ of arc or better. Both subjects were strongly left-handed.

Apparatus

Subjects sat at a table (100 cm wide and 61 cm deep) with a matte black surface. A circular, 1-cm-diameter microswitch button located 15 cm directly in front of the subject functioned as the start position for each reaching movement. A circular fluorescent lamp was suspended approximately 80 cm above the table surface. This lamp was illuminated by the experimenter from a remote switch that also triggered the start of data collection.Six different Efron blocks (ranging in width from 2.5 cm to 5 cm but with the same overall surface area) were placed at one of six different distances (ranging from 20 to 45 cm from the observer). Only the grasping movements made to the middle three sizes (3 cm to 4 cm) were examined at the 20, 30 and 40 cm distances, with the other size×distance combinations used as distracters. The objects were positioned with their long axis perpendicular to the body's mid-sagittal plane. The underside of each of the objects contained an embedded magnet which, when placed in position, closed one of three magnetic switches located under the table surface at distances of 20, 30 or 40 cm from the microswitch along the subjects' midline. When a subject picked up the object, contact between the two magnets was broken, signalling the end of collection for a given trial.

Three 4-mm-diameter infrared light-emitting diodes (IREDs) were attached with small pieces of cloth adhesive tape to the head of the radius at the preferred wrist, the ulnar border of the thumbnail on the preferred hand, and the distal border of the index fingernail on the preferred hand. The tape allowed complete freedom of movement of the hand and fingers.

The IREDs were monitored by two high-resolution infrared-sensitive cameras positioned approximately 2 m from the subject. The positions of the IREDs were digitized at a rate of 100 Hz into two-dimensional coordinates and then passed on to the data collection system of a WATSMART computer (Waterloo Spatial Motion Analysis and Recording Technique, manufactured by Northern Digital, Waterloo, Ontario). Stored sets of two-dimensional coordinates were converted into three-dimensional coordinates off-line and filtered (with a low-pass second-order Butterworth filter with a 7-Hz cut-off).

Procedure

At the beginning of the test session, subjects were given the handedness questionnaire and tested for eye dominance (viewing preference) and stereoacuity (Randot stereotests). Subjects were then seated at the testing table and instructed to pick up the target object with the thumb and index finger of their preferred hand across the narrow part of the block as soon as they could see it after the overhead light was illuminated. They were instructed to reach as quickly, accurately and 'naturally' as possible.At the beginning of each trial, subjects placed the tips of the index finger and thumb of their preferred hand on the start button. Between trials, the room lights were extinguished and subjects were instructed to keep their eyes closed during this time. Once a block had been placed in a given position by the experimenter, subjects were given a verbal signal to open their eyes and the overhead light was turned on, which started the collection of the trial.

Subjects were administered testing blocks of 55 experimental trials, each consisting of five instances of each of the nine Distance×Object Size combinations that were analysed along with ten additional trials with other Distance×Object Size combinations.

Trial presentation was random and each testing block was preceded by a series of five practice trials. Each subject performed one block of binocular presentation trials and one block of monocular presentation trials. In the monocular presentation trials, subjects wore an eye-patch over their non-dominant eye. The viewing condition blocks were counterbalanced between subjects. Any experimental trial in which the subject dropped an object was repeated at the end of a given block. The testing session lasted for approximately 60 min.

Dependent measures

Maximum grip aperture (the maximum vectored distance between the thumb and index finger IREDs), movement duration of the reach (calculated by subtracting the movement onset time from the time at which an object was lifted, breaking the magnetic switch) and maximum velocity of the reach were computed from the three-dimensional coordinates.

Results

Under normal binocular viewing conditions, both DF and JW, like the control subjects, showed excellent scaling of their maximum grip aperture as a function of object size (Fig. 1). When only monocular viewing was permitted, the control subjects continued to show accurate scaling for object size (see Fig. 1B and D for age- and sex-matched control data). DF also continued to show evidence of scaling although the trial-to-trial variance of her maximum grip aperture increased noticeably under monocular viewing (Fig. 1A). JW's performance

deteriorated dramatically and he no longer showed evidence of scaling (Fig. 1C), although as we shall see he remained sensitive to some aspects of the goal object. Thus, unlike the control subjects, the visuomotor performance of the two individuals with visual form agnosia was quite sensitive to the removal of binocular vision. In addition to showing good scaling for object size, the control subjects also showed excellent size constancy in both binocular and monocular viewing conditions; in other words, they opened their hand the same amount for a particular object independent of the distance of that object. As Fig. 2B and D illustrate, the slopes of the lines describing mean grip aperture as a function of distance for the two age-, handedness- and sex-matched control subjects did not differ significantly from zero in either condition ($P>0.05$). Under binocular viewing conditions, DF also showed normal size constancy in her grasp and, like the control subjects, the slope of the line describing her grip aperture as a function of distance ($y=-0.003x+97.15$) did not differ significantly from zero [$t(43)=0.04$, $P>0.05$]. Under monocular viewing conditions, however, her behaviour was very different (Fig. 2A). With one eye covered, she no longer showed size constancy and opened her hand significantly wider for objects that were closer to her – objects that would have had larger retinal image sizes. In this case, the slope of the line describing the aperture-distance function ($y=-0.28x+108.04$) was significantly different from zero [$t(43)=2.96$, $P<0.01$]. JW also showed normal size constancy in his grasp under binocular viewing conditions

Fig. 1A–D The effects of viewing condition on maximum grip aperture across object width for **A** the patient DF, **B** the control subject LW, **C** the patient JW and **D** the control subject RK (*error bars* SEMs, *open circles* monocular viewing condition, *open squares* binocular viewing conditions)
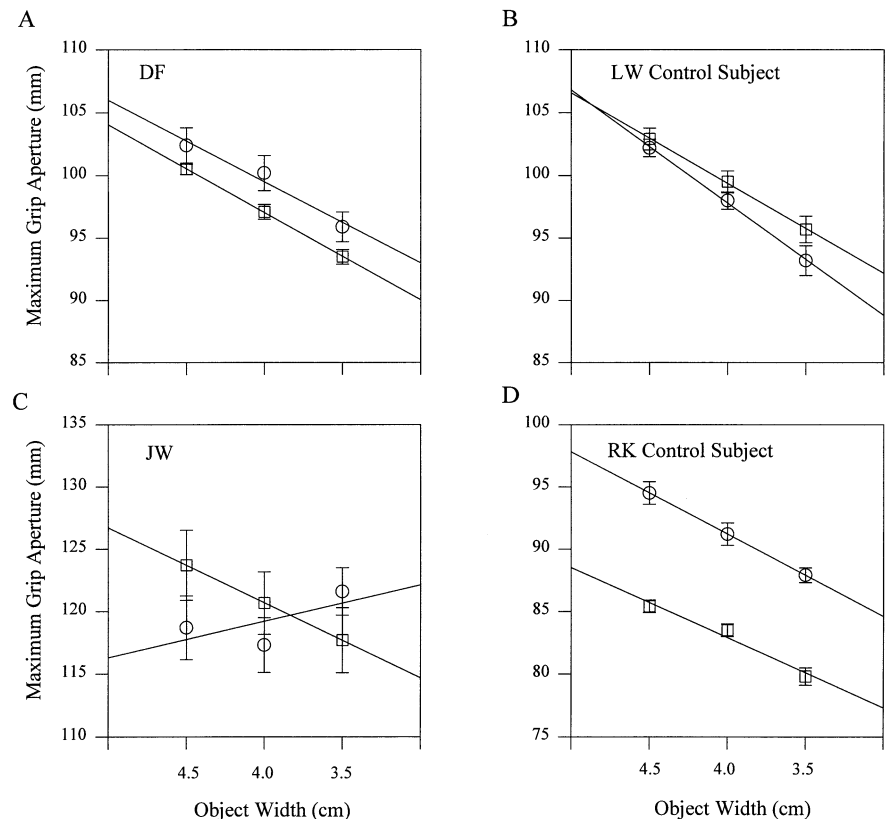
118

Fig. 2A–D The effects of viewing condition on maximum grip aperture across object distance for **A** the patient DF, **B** the control subject LW, **C** the patient JW and **D** the control subject RK (*error bars* SEMs, *open circles* monocular viewing condition, *open squares* binocular viewing conditions)
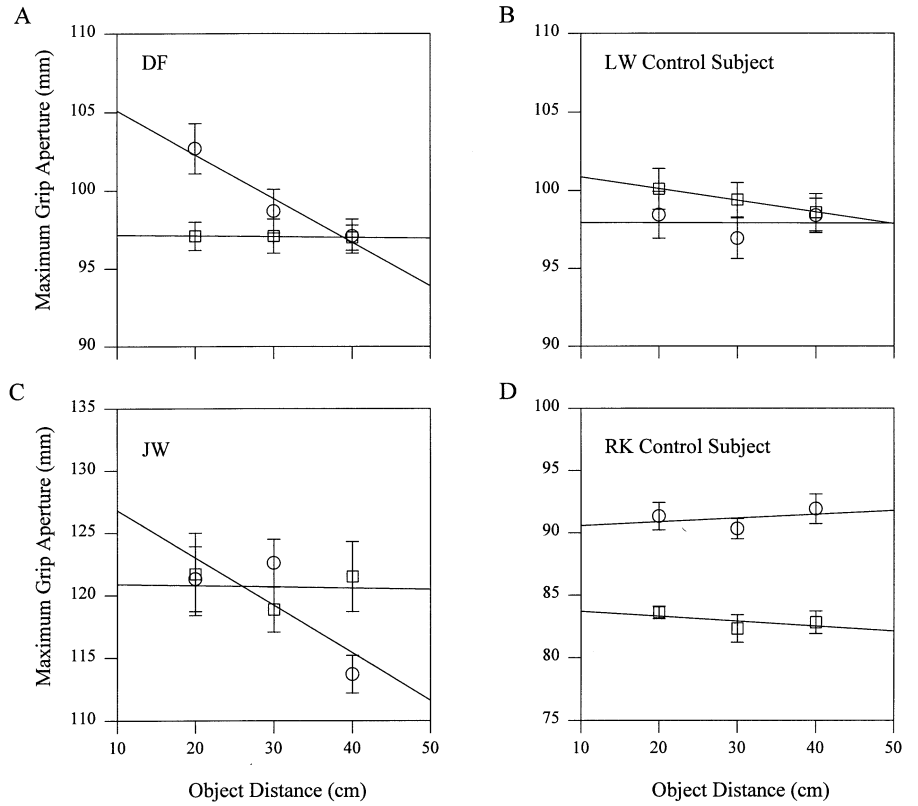

Fig. 3A–D The effects of viewing condition on movement duration across object distance for **A** the patient DF, **B** the control subject LW, **C** the control subject KN and **D** the control subject AH (*error bars* SEMs, *open circles* monocular viewing condition, *open squares* binocular viewing conditions)
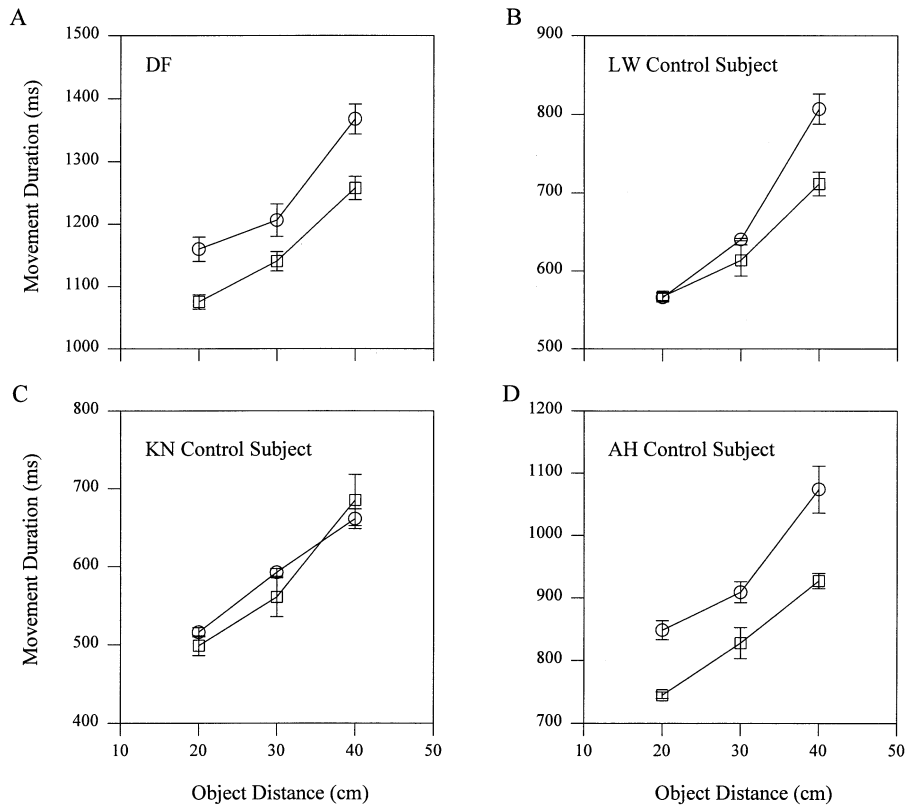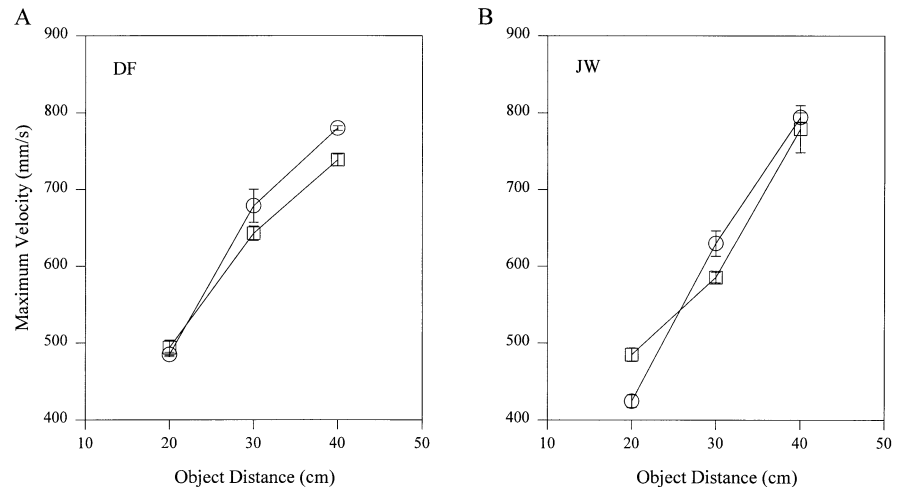
Fig. 4A, B The effects of viewing condition on maximum velocity across object distance for **A** the patient DF, and **B** the patient JW (*error bars* SEMs, *open circles* monocular viewing condition, *open squares* binocular viewing conditions)

[$y=-0.008x+120.94$, $t(43)=0.04$, $P>0.05$], but again under the monocular viewing conditions he opened his hand significantly wider for objects that were closer to him [$y=-0.38x+130.58$, $t(43)=2.53$, $P<0.02$] (Fig. 2C).

Although DF and JW, unlike their control subjects, showed a deterioration in the calibration of grip aperture when binocular information was removed, the effects of monocular viewing on the reach itself were similar in both the patients and the control subjects. For example, as Fig. 3 shows, duration increased with increased object distance in DF and her three control subjects under both binocular and monocular viewing conditions. Moreover, as Servos et al. (1992) originally observed, there was a tendency for movement durations to be longer when only monocular cues were available. Although JW showed a similar increase in movement duration with object distance under both binocular and monocular viewing conditions, the typical increase in movement duration with monocular viewing was not observed. Finally, as Fig. 4 shows, both DF and JW, like the control subjects and like subjects in earlier experiments (e.g. Servos et al. 1992), showed a systematic increase in velocity with object distance under both viewing conditions. In short, distance scaling for reach kinematics in DF and JW, unlike grip calibration, seemed rather refractory to the removal of binocular information.

Discussion

The fact that size-constancy in grip aperture is disrupted in DF and JW by the removal of binocular cues suggests that these cues are of primary importance in calibrating their grip aperture to the true size of the goal object when it is presented at different viewing distances. This result, combined with earlier observations in normal subjects (Servos et al. 1992), suggests that binocular information plays a critical role in normal human prehension. When calibrating the grasp, information about distance derived from stereo and/or convergence is combined with information from the size of the retinal image of the

goal object (which will vary systematically with viewing distance). But as we emphasized in the Introduction, when such information is denied to them, normal subjects are able to fall back on the many pictorial cues available in the scene – cues to which DF and JW are apparently insensitive. Such cues include linear perspective cues from the table, familiar size, the change in the object's shape and aspect ratio with viewing angle, elevation of the object in the scene, shading and shadows, all of which are still available under monocular viewing conditions. As we saw earlier, however, these cues are not primary for the control of grasping and, if binocular information is available, the generation of a well-calibrated grasp will be unaffected by the introduction or removal of pictorial information. If one assumes that the visuomotor systems mediating grasping in DF and JW are relatively intact, then their poor grasping performance under monocular viewing suggests that pictorial information may normally reach visuomotor control systems only via the ventral stream networks that mediate the experiential perception of visual scenes – networks that are damaged in these patients. In other words, if one assumes that the visuomotor systems mediating prehension do not have independent access to the pictorial cues processed by perceptual mechanisms, then DF and JW would be unable to make full use of the pictorial scene cues that remain available when binocular cues are removed. As a result, they would have to rely on a retinal image size that remains uncalibrated for distance, which leads them to open their hand wider when reaching for objects closer to them, objects that subtend larger retinal image sizes.

Despite her failure to show size-constancy in grip scaling, DF continued to demonstrate some sensitivity to the dimensions of the goal object under monocular viewing conditions. Thus, the wider the block placed in front of her, the wider she opened her hand in flight. Nevertheless, she showed considerable trial-to-trial variability, reflecting the fact that her grasp was also increasing in size with the increase in the size of the retinal image that occurred when the object was positioned at a closer dis-

tance. The consistent pattern of performance observed in DF was not seen in JW. His grip scaling deteriorated markedly under monocular viewing conditions – even though, like DF, he showed evidence of scaling, albeit less reliable than hers, under binocular viewing conditions. When he was allowed only a monocular view, he seemed unable to use the dimensions of the different goal objects to calibrate his grasp. Nevertheless, JW showed some sensitivity to retinal image size under monocular viewing since he opened his hand wider for closer objects. It remains unclear as to why grip scaling in DF is so much better than in JW. The difference could reflect a difference in the extent of brain damage. In JW, the lesion extends more into parietal cortex than it does in DF. But the difference in performance could reflect more than simply the extent or location of lesions in the two subjects. DF has had much more experience than JW in the kind of experimental setting we used. DF has been tested two or three times each year over the last 8 years while JW has been tested only twice in this situation.

The apparent scaling of grasp in DF (but not in JW) under monocular viewing conditions could be construed as evidence that she is still able to use pictorial cues to calibrate her grasp. It should be remembered, however, that the use of retinal image size, even when improperly calibrated, will result in a systematic relationship between object size and grip aperture. In other words, at any one distance the largest block will always subtend the largest retinal image size. Therefore, the mechanism in DF's visuomotor system that normally integrates retinal image size and distance could still generate larger apertures for larger retinal image sizes but these outputs would not be calibrated for distance because binocular distance cues are unavailable. This would be particularly likely in an experienced subject such as DF who is familiar with the blocks that we use and the dimensions of the testing surface on which they are placed. Nevertheless, we cannot exclude the possibility that her superior performance is due to the fact that her access to pictorial cues is simply not as disturbed as that of JW.

One paradox in the results remains to be discussed. Although the calibration of grip size in DF and JW was affected by the removal of binocular cues, the kinematics of the reach itself were largely unaffected. In other words, even under monocular viewing conditions they were still able to use distance information to compute the required amplitude of their reach. What cues could they be using? Despite their profound form perception deficit, DF and JW can still detect the movement of objects and contours in the visual array (Milner et al. 1991; unpublished observations). It is possible, therefore, that they are able to use retinal motion (from head movements) to compute distance for transporting the limb to the correct location – even though this cue was not used (and perhaps could not be used) to calibrate their retinal image size. As a consequence, they would reach to the right location but their grip aperture would remain incorrectly calibrated. It is possible, but much less likely, that the spared visuomotor networks in DF and JW are able to use pictorial scene cues to calibrate the trajectory of the reach but not the amplitude of the grasp. Finally, it is possible that they were using the large changes in the retinal image size of the goal object that occurs with varying distance to calibrate their reach. Although it might seem surprising that distance cues can be used reliably to program and control a reaching movement but not the grasp, these components of prehension have been shown to depend on rather different computations and to be mediated by different neural networks within the dorsal stream (for review see Jeannerod 1988; Milner and Goodale 1995).

In summary, an efficient grasp requires rapid and accurate computations of the size, shape, orientation, and location of the object. When binocular distance cues are removed, individuals with normal vision, unlike patients with visual form agnosia, are able to use scene-based pictorial cues to calibrate the retinal image size of the goal object so that the grasp can be scaled to the true size of the object. The failure of individuals with visual form agnosia to scale their grasp appropriately under the monocular viewing condition, despite showing normal binocular grasping, suggests that pictorial cues to depth, which are presumably processed by mechanisms mediating our perception of objects and events in the world, can be accessed by visuomotor mechanisms only indirectly. In short, the visuomotor system 'prefers' to use binocular information and uses pictorial cues only as a last resort.

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