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Grasping the non-conscious: Preserved grip scaling to unseen objects for immediate but not delayed grasping following a unilateral lesion to primary visual cortex

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ABSTRACT

Patients with damage to primary visual cortex can sometimes direct actions towards 'unseen' targets located in areas of the visual field that are deemed 'blind' on the basis of static perimetry tests. Here, we show that a patient with a complete right homonymous hemianopia after a V1 lesion remains sensitive to the width of objects presented in her blind field but only when reaching out to grasp them in 'real-time'. A subsequent fMRI experiment revealed spared extra-geniculostriate pathways, which may mediate her preserved abilities. Taken together, the results support the view that visually guided movements can be mediated by pathways that do not support visual consciousness.

1. Introduction

The deceptively simple act of reaching out and grasping an object is an almost perfect example of what the brain has evolved to do: namely, to control our movements in the world. Vision plays an indispensable role in this skilled behavior, and over the last three decades, considerable effort has been spent trying to understand the neural substrates of visually-guided grasping. In 1992, Goodale and Milner proposed that the ventral visual processing 'stream' that arises from early visual areas and projects to inferotemporal cortex mediates the recognition and identification of goal objects for action, while the dorsal visual processing stream that arises from early visual areas and projects to the posterior parietal cortex (PPC) transforms the particular information about the goal object into the required motor coordinates for action. According to their account, the division of labour between the ventral and the dorsal pathways reflects the different requirements of vision-for-perception and vision-for-action respectively.

Visual recognition depends on object constancy, the ability to identify the same object from different viewpoints, whereas the visual control of action requires that the visuomotor transformations reflect the disposition of the goal object with respect to the actor at the precise moment the action is performed. Thus, Goodale and Milner argue, because the dorsal stream computes visuomotor transformations *de novo* each time an action is performed, it has no need for long-term memory. In fact, storing particular visuomotor coordinates would be counterproductive since the disposition of the goal object with respect to the effector to be used can change dramatically in just a few seconds. In stark contrast, visual processing in the ventral-stream interacts with long-term memory stores of early visual experiences to enable the recognition of objects over long periods of time. This means that actions that are performed on remembered objects that are no longer visible must invoke stored visual information originally processed by the ventral stream (for a discussion of these issues, see Milner & Goodale (2006)).

One principal line of evidence for Goodale and Milner's (1992) proposal comes from work with patients with visual form agnosia and optic ataxia. They have argued that the different patterns of spared visual abilities and deficits in these two patient groups constitute a functional and anatomical double dissociation between vision-for-perception and vision-for-action. Patient DF, for example, who has visual form agnosia as a result of damage to the lateral occipital complex (LOC), a ventral-stream structure (James, Culham, Humphrey, Milner, & Goodale, 2003), is still able to reach out and grasp objects accurately despite the fact that she is unable to report either manually or verbally their size, shape, or orientation. Thus, DF is unable to use her finger and thumb to reliably indicate the width of a target object when asked to give an estimate of its size, but when she reaches out to grasp that same object her grip

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aperture (the distance between her finger and thumb) smoothly scales in-flight to the object's width (Goodale, Milner, Jakobson, & Carey, 1991; see also patient JS: Karnath, Ruter, Mandler, & Himmelbach, 2009). The authors argued that her preserved ability to process visual information about object size, shape, and orientation for the purposes of target-directed actions is mediated by a largely functioning and intact dorsal stream. Importantly, if DF is asked to reach out and grasp an object that she saw only moments before, her performance completely deteriorates and she no longer shows any evidence of grip scaling (Goodale, Jakobson, & Keillor, 1994). This impairment in memory-driven grasping is thought to reflect the fact that, because of her ventral-stream damage, she was unable to perceive the dimensions of the object and store that information in memory for later explicit use.

Optic ataxia is a visuomotor disorder that impairs target-directed actions, such as reaching and grasping. It typically arises following damage to the dorsal stream, particularly in the superior parietal lobule (SPL), intra-parietal sulcus (IPS), and parietal–occipital cortex (POC) (Karnath & Perenin, 2005; Perenin & Vighetto, 1988). Nevertheless, because the ventral stream often remains relatively intact in these patients, they perform reasonably well on perceptual tasks that require object localization, identification, or discrimination (Goodale, Meenan et al., 1994; Jeannerod, 1988; Jeannerod, Decety, & Michel, 1994; Jakobson, Archibald, Carey, & Goodale, 1991; Perenin & Vighetto, 1988). Thus, these patients can accurately estimate the size of target objects (Jeannerod et al., 1994) and yet show profound deficits in grip formation and coordination when asked to grasp them (Jakobson et al., 1991; Jeannerod et al., 1994; Milner et al., 2001; Perenin & Vighetto, 1988). Remarkably, if the task is modified to require the patient to grasp an unseen object viewed 2 s before the response is cued, their performance improves (Milner et al., 2001; Rossetti et al., 2005). As Milner et al. (2001) noted, these results are consistent with the observation described earlier that DF's performance on a similar task was severely impaired (Goodale, Meenan et al., 1994a). Taken together, these results suggest that skilled target-directed actions depend on intact dorsal-stream structures in which the visual inputs are processed at the moment an action is programmed, and that actions that follow a delay must be programmed on the basis of remembered visual input which ultimately depends on an intact and functioning ventral stream.

Although patient DF is able to scale her grip aperture to objects that she cannot recognize, it is unclear what remaining visual pathways are responsible for this remarkable ability. Retinal inputs to primary visual cortex (V1) via the geniculostriate pathway are known to innervate structures in the dorsal stream. It may be the case that this pathway is critical for DF's preserved visuomotor abilities, particularly since DF's V1 appears to be intact (James et al., 2003; Milner et al., 1991). In fact, because not all of her ventral stream is damaged, DF has some spared perceptual abilities. She can, for example, give explicit (and often detailed) reports of the surface properties of objects signaled by their color, visual texture, and specular highlights (Humphrey, Goodale, Jakobson, & Servos, 1994). It is important to emphasize once more, however, that she cannot give such reports of their shape and geometry.

Although inputs from V1 may well be responsible for the preserved visuomotor abilities in patients with visual form agnosia, there have been reports of similarly preserved visuomotor abilities in patients with visual field loss who do not have access to any conscious vision following damage to V1. Specifically, Weiskrantz and colleagues (Sanders, Warrington, Marshall, & Weiskrantz, 1974; Weiskrantz, Warrington, Sanders, & Marshall, 1974) coined the term "blindsight" to describe patients with visual field loss who deny seeing visual stimuli presented in their affected field but whose voluntary performance can be reliably influenced by visual stimulation. This group was the first to show that a patient, DB, with hemianopia in his left visual field could accurately locate targets presented in his blind field by pointing to them. Weiskrantz later showed that DB could localize targets accurately when they were presented in the regions of his blind field outside of his optic disc or 'blind spot' (Weiskrantz, 1987). This suggests that light scatter and poor fixation could not account for DB's accuracy, since either of these factors would be equally applicable to a stimulus presented in his blind spot. Just 1 year prior to Weiskrantz's findings, Poppel, Held, and Frost (1973) showed that four patients with quadrantanopia (as determined with static perimetry) could scale the amplitude of their saccades to a spot of light flashed briefly (100 ms) on any one of the three closest target positions that fell along an oblique meridian within the scotoma. A number of additional studies have shown that some (not all) patients retain residual processing in the blind regions of their visual field and can reliably process stimuli presented in their affected field during speeded detection tasks (Corbetta, Marzi, Tassinari, & Aglioti, 1990; Marzi, Tassinari, Aglioti, & Lutzemberger, 1986) and forced response tasks like discrimination (e.g., Weiskrantz, , 1986, 1987) and target localization with either manual pointing (e.g., Corbetta et al., 1990; Danckert et al., 2003; Perenin & Jeannerod, 1975, 1978), or eye movements (e.g., Barbur, Forsyth, & Findlay, 1988; Poppel et al., 1973).

Patients with hemianopia show a range of spared visuomotor abilities that are not restricted to saccades and target localization. In particular, the ability to act on 'unseen' objects has been termed 'action blindsight' (Rossetti & Pisella, 2002; see also Danckert & Rossetti, 2005). Some patients, for example, can reliably calibrate their in-flight grip aperture to the size of novel objects located in their blind field when reaching out to pick them up (Jackson, 1999; Marcel, 1998; Perenin & Rossetti, 1996) (for recent reviews see Cowey, 2010; Danckert & Rossetti, 2005). Perenin and Rossetti (1996) showed that patient PJG with hemianopia could scale his grip aperture to the width of the objects presented entirely within his blind field yet he could neither 'match' the object's size using his thumb and forefinger nor verbally discriminate the objects according to their size. Marcel (1998) tested two patients, one of whom was GY, both of whom scaled their grip, categorically at least, to the diameter of large and small variants of a cylinder and circle. In contrast to Marcel's findings, Jackson (1999) later found that patient GY could not scale his grip aperture to the size of objects presented entirely within his blind field. Nevertheless, GY did show grip scaling to variations in the size of objects when they extended into his sighted field – even though the part of the object that was visible did not change in size from trial to trial. Interestingly, however, with the same display, GY failed to estimate the magnitude of the (unseen) relevant dimension of the objects accurately on a verbal scale of one to six. In addition, recent studies have also shown that patients with blindsight can avoid unseen obstacles (de Gelder et al., 2008; Striemer, Chapman, & Goodale, 2009). In short, several studies have demonstrated that patients with action blindsight can carry out rather complex actions in the absence of any conscious vision. Thus, examining patients with action blindsight affords the opportunity to investigate what aspects of dorsal stream function remain in the absence of inputs from V1.

The existence of action blindsight suggests that intact visual pathways outside of the prominent geniculostriate pathway are capable of mediating visually guided actions. One such pathway from the retina courses through the superior colliculus (SC) and pulvinar nucleus in the thalamus (i.e., the retino-tectal-pulvinar pathway) to the motion-sensitive area MT and from there onto areas in the dorsal stream. This pathway is known to convey primarily magnocellular information which has relatively low spatial resolution but is extremely sensitive to changes in contrast. Recently, a direct projection from the eye to the pulvinar, and then to MT has been identified in the marmoset (Warner, Goldshmit,

& Bourne, 2010). In addition, there are projections from koniocellular cells in the interlaminar regions of the dorsal lateral geniculate nucleus (dLGN) that bypass V1 and project directly to area MT and onward to other regions of the dorsal stream (Sincich, Park, Wohlgemuth, & Horton, 2004; for review see Vakalopoulos, 2005). The koniocellular cells in the dLGN tend to convey information that is similar to that conveyed by the cells in neighboring parvocellular or magnocellular layers (Hendry & Reid, 2000). A recent study in monkeys with V1 lesions suggests that the projections from the interlaminar regions of the dLGN are capable of mediating some residual visual behavior (including saccades). Specifically, these residual abilities, and the associated BOLD activation in area MT and extrastriate cortex disappeared when the dLGN was reversibly inactivated (Schmid et al., 2010). Thus, in the absence of V1 input, there appears to be a number of extra-geniculostriate pathways that could continue to provide information about targeted objects to the dorsal stream upon which the transformations required for calibrating grip aperture could be based.

In the current set of experiments, we replicate and extend Perenin and Rossetti's (1996) original demonstration that a patient with a hemianopia (patient PJG) was capable of scaling a grasping movement directed towards an 'unseen' object presented in the blind field. We tested a new patient SJ, who has a complete right homonymous hemianopia as a consequence of a stroke in her left occipital cortex. Not surprisingly, patient SJ, like patient PJG, was unable to estimate the widths of objects presented in her blind field. Nevertheless, she did show evidence of blindsight: she could localize 'unseen' stimuli presented in her blind field, and could scale her in-flight grip to the widths of novel objects located in her blind field when reaching out to pick them up. Importantly, however, she could do this even when vision was not available during the execution of the grasp. But for grip scaling to occur with objects in her blind field, the movements had to be programmed and initiated while vision was available (i.e., in real-time). When a brief delay was introduced between last viewing the object and programming the movement, SJ showed no evidence of grip scaling. Finally, we report the results of a functional magnetic resonance imaging (fMRI) study with SJ that provides tentative support for the idea that her spared abilities are mediated by pathways to extrastriate cortex that bypass V1. Taken together, these data contribute to a growing body of evidence that visuomotor networks in the dorsal stream can operate independently of input from V1, but only in real-time on a moment-to-moment basis.

2. Session 1: methods

2.1. Participants

Patient SJ is a 37 year-old right-handed female who has a complete right homonymous hemianopia with no macular or temporal crescent sparing following a left posterior cerebral artery stroke which occurred 7 years prior to the time of testing. Her lesion, as revealed by high-resolution MRI, is restricted to the left occipital lobe and optic radiations with some extension into the parahippocampal gyrus (Fig. 1a) with a small remaining "tag" of cortex visible at the occipital pole. Visual fields were assessed by a neuro-ophthalmologist (D. Nicolle) using a Goldman Perimeter with III-4 sized targets (Fig. 1b). Informed consent was obtained from SJ and all experimental procedures were approved by the University of Western Ontario Health Sciences Research Ethics Board and in full accordance with the Declaration of Helsinki.

Although patient SJ is completely blind in her right visual field on static perimetry, she reports subjective sensations of motion. Informal testing found that SJ was extremely accurate at indicating whether the experimenter's hand waved or not while he stood facing her across the table in her blind field and a second experimenter monitored her eyes. SJ's description of the phenomenon was not that she could see the hand but that she detected a perturbation of a 'field' of haze located in her blind field whenever the hand moved. Her subjective report suggests that she possesses a form of Riddoch phenomenon, which refers to a patient's ability to sense when a visual stimulus is moving within their scotoma but not when the stimulus is stationary (Riddoch, 1917).

In addition to patient SJ, we also tested 12 right-handed control participants (M = 29 years, SD = 7.4 years) with normal or corrected-to-normal vision and no prior neurological history. Note that the control participants performed the grasping and manual matching tasks under the same conditions as patient SJ but with fewer trials and in only one test session, rather than two. We did not test the control participants on the preliminary target-detection and target-localization tasks.

2.2. Experimental setup and design

2.2.1. Target-localization

Patient SJ sat 40 cm away from a touch screen monitor (32″ LCD, Mass Multimedia Inc; refresh rate 60 Hz) and fixated on a cross located at the center of the touch screen. The touch screen recorded the point on the screen where SJ's finger first landed (end-point) for each trial. The target was a black circle (2.2 cm diameter), which subtended approximately 3° of visual angle presented for 100 ms at one of four horizontal eccentricities from fixation (10°, 17°, 24°, or 30°) on a uniform grey background. Each target position was sampled 20 times, and the trial order was pseudo-randomized for target position. The time from trial onset to target onset was randomly varied from 1 to 3 s (in 500 ms increments) to minimize the predictability of target onset and the incidence anticipatory responses. SJ's eye movements were monitored 'online' (and recorded for additional evaluation 'offline') by an experimenter using a video camera zoomed-in on one of her eyes, while a second experimenter advanced the trials. SJ was excellent at fixating and very few trials had to be discarded because of eye movements.

2.2.2. Explicit target-detection

We also tested patient SJ on the redundant target paradigm. This target-detection task requires the participant to respond with a button press as soon as a target appears on the screen. Typically, participants are faster to respond to two targets presented simultaneously than only one (Marzi et al., 1986). This phenomenon, known as redundancy gain, has been linked with the retino-tecto-pulvinar pathway which is thought to mediate blindsight observed in some patients with hemianopia or hemispherectomy (Corbetta et al., 1990; Leh, Johansen-Berg, & Ptito, 2006; Leh, Mullen, & Ptito, 2006; Leh, Ptito, Schonwiesner, Chakravarty, & Mullen, 2009; Marzi, Mancini, Metitieri, & Savazzi, 2009) and has revealed residual visual processing in some, though not all, patients (Leh, Ptito et al., 2006; Marzi et al., 1986). Patient SJ sat 40 cm away from a 32″ LCD touchscreen with her head resting in a chin-rest. The target was a black circle (2.2 cm diameter), which subtended approximately 3° of visual angle presented for 100 ms on a uniformly grey background. On a given trial, the target could appear 10° of visual angle to the left or right of a fixation cross located at the center of the screen, on both sides, or not at all. Thus, there were four conditions total. Two 'single target' conditions (left or right hemi-field), one 'double target' condition (two targets presented simultaneously, one in each hemi-field), and a blank condition ('catch' trials) on which no target was presented. The task was administered in four separate blocks of 40 trials (four conditions, 10 trials per condition). Trials were presented in a pseudo-random sequence and the time between the onset of the

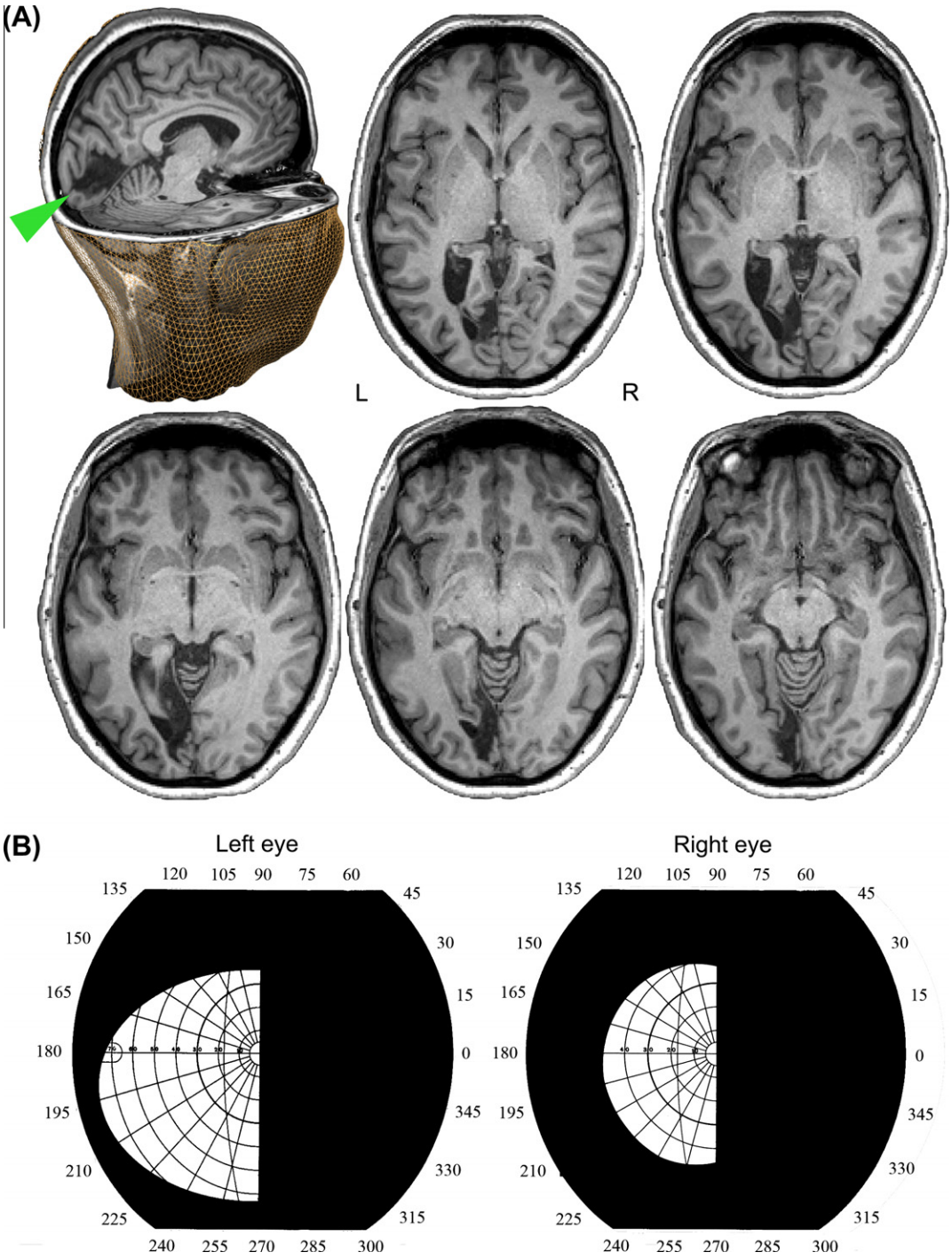

Fig. 1. Panel A depicts a saggital and a series of axial slices from a T1-weighted high resolution (192 slice 1 mm iso-voxel) anatomical MRI scan of patient SJ's left occipital lesion recently obtained from a 3 Tesla Siemens Tim-Trio MRI scanner at the Robarts Research Institute (London, Ontario, Canada). The lesion is restricted to the left occipital lobe and optic radiations with a minor extension into the parahippocampal gyrus. The green arrow indicates the spared "tag" of cortex located at the occipital pole. Panel B depicts the results of the visual field testing with SJ. SJ has a complete right hemianopia with no macular or temporal crescent sparing. Data are presented separately for the left and right eyes.

trial and the onset of the target(s) was randomized to last anywhere from 1 to 3 s (in 500 ms increments). A tone was not used for this task, since SJ was required to respond only when she saw a target.

2.2.3. Grasping

Targets stimuli were four wooden objects each of which was 1.5 cm in height, 5 cm long, and differed from the others only in width. The smallest object width was 2.0 cm with each successively larger object's width incremented by 1.5 cm to a maximum of 6.5 cm. The objects were painted flat black to reduce intra- and extra-ocular dispersion and were padded on the bottom to minimize the sound of contact with the surface of the table on placement. The table top was covered with white Bristol board to provide a high contrast between the table surface and the black objects. Patient SJ was seated in front of the table with her head positioned in a chin-rest. The chin-rest was attached to the table edge directly in front of the start button, which was 15 cm from

the table edge. SJ aligned her midline with the start button and the chin-rest. The fixation target was centered 30 cm directly ahead of the start button and approximately 50 cm from the participant's eyes. The inner edge of the objects was placed 8 cm either to the left or to the right of fixation, which corresponded to 9° of visual angle to the left or to the right of fixation. The reach-distance from the start button to the center of the edge of the objects facing SJ was approximately 32 cm.

Patient SJ's vision was controlled during the grasping session with a pair of PLATO goggles (Translucent Technologies, Toronto, Ontario) worn by the participant. The goggles are equipped with liquid crystal lenses that can switch between opaque and transparent states in less than 6 ms. As for the target-localization task, SJ's eye movements were monitored 'online' continuously by one experimenter and recorded for additional evaluation 'offline' using a video camera zoomed-in on one of her eyes, while a second video camera recorded her movements.

Patient SJ's performance on visually-guided grasping was tested in blocks of 49 trials (33 trials for the control participants) administered first in the left visual field and then in the right visual field. Specifically, one block of trials was administered to test SJ's performance with her left hand for objects located in her sighted (left) visual field, and two subsequent blocks of trials were administered to test SJ's performance with her right hand for objects located in her blind (right) visual field. This was done because of the expected difference in effect size between the two fields. Within each block of 49 trials object size was pseudo-randomized such that each object appeared at least 12 times and had an equivalent probability of being preceded or followed by any of the objects. In addition, no object was permitted to occur more than twice consecutively. Thus, the trial order prevented the experience of grasping any particular object on preceding trials from systematically influencing SJ's performance on any subset of the objects. This precaution seemed particularly relevant following recent studies that have shown that the trial history of visual feedback (Whitwell & Goodale, 2009) and indeed that of object size (Dixon & Glover, 2009) can systematically influence grip aperture. The positions of three infrared emitting diodes (IREDs) were recorded in three-dimensional space by Optotrak 3020 (NDI, Waterloo, Ontario) at 200 Hz (one frame every 5 ms) for 3 s following the response cue. One IRED was attached to the tip of the thumb, a second was attached to the tip of the forefinger, and a third attached to her wrist. The IREDs were positioned such that the pads of the forefinger and thumb were unobstructed.

2.3. Procedure

2.3.1. Target-localization

First, the touchscreen was calibrated to ensure veridical endpoint measurements. To calibrate the participant's eye movements on the camera monitor, one of the experimenters asked the participant to fixate on the central cross and then noted the position of SJ's iris on the camera display. The experimenter then asked SJ to fixate on the target closest to the fixation cross and again noted the position of SJ's iris on the camera display. Eye-movements of 2° could be readily detected using this method, which was used in all the experiments, including those with the control participants. For the target-localization task, each trial began with the target stimulus presented in one of four pre-determined locations for 100 ms coinciding temporally with a 1000 Hz tone. The tone cued SJ to both look and point to the target's location. SJ used her forefinger to touch the screen where the target had been presented. Before and after each pointing movement, SJ kept the tip of her forefinger resting on a start position. Her performance was tested in her sighted (left) and then in her blind (right) visual field. SJ was excellent at maintaining fixation.

2.3.2. Explicit target-detection

Patient SJ fixated centrally on a cross and pressed a button as soon as she saw a target appear anywhere on the screen. SJ insisted she did not see any targets in her blind (right) visual field with the exception of two discarded single-target trials on which she failed to maintain fixation.

2.3.3. Grasping

Patient SJ was asked to maintain fixation throughout the test session. The goggles restricted her vision between trials, which allowed the experimenter to place the object for the next trial out of sight from SJ. This also meant that SJ could not see the fixation target between trials and as a result she was asked to maintain her gaze as best she could by visualizing the fixation target. Before testing commenced, the experimenters explained the nature of the tasks and administered several practice trials to familiarize her with the events and the pace from trial to trial. Throughout these practice trials, SJ reported no difficulty maintaining her gaze on the unseen fixation target between trials. Nevertheless, as mentioned previously, one experimenter monitored her eye movements 'online' on the display of a video camera that was zoomed-in on one of her eyes. A second experimenter concerned himself with placing the objects and observing SJ's performance. Trials during which SJ appeared to move her eyes, fumbled the object, or initiated her movement too early were noted and repeated at the end of the block.

Before the onset of a trial and at the end of each trial, patient SJ depressed the start button with the tips of her thumb and forefinger pinched together while keeping her other hand resting on her lap below the surface of the table. The experimenter initiated each trial which began with a 1 s delay followed by a trigger that switched the lenses from their default opaque state to their transparent one, which permitted SJ a view of the workspace with the object located in either her sighted (left) or blind (right) visual field. SJ was instructed to initiate her movement when she could see the workspace (i.e., when the goggles opened). Patient SJ was asked to reach out and pick the object up off the surface of the table using only her forefinger and thumb such that contact with the object meant that her grip opposition axis spanned the width of the object. The lenses remained transparent for 1 s following the release of the start button which permitted SJ a full view of the workspace that included the time taken to obtain the object (i.e., closed-loop visual feedback). Note that there was no need to employ a tone "go" cue for this task, since SJ could register a change in the visual input in her sighted (left) visual field as soon as the goggles opened. This was not the case for target-detection and target-localization tasks, but only the target-localization task required SJ to respond on each trial. Finally, during testing the experimenters periodically asked SJ if she could see any of the objects in her blind field to which she answered that she could not.

2.4. Data processing and statistical analysis

We used ordinary least squares (OLS) linear regression to model the raw dependent measures as linear functions of the independent variables for each field and kinematic task separately using SPSS version 17.0 (Chicago, Illinois). In addition to the Pearson product-moment correlation (correlation coefficient), r, we report the unstandardized regression coefficient, b, for two reasons. First, the dependent and independent variables share the same units within each behavioral task administered. In general, b represents the change in the dependent measure per incremental increase in the independent variable while holding all other modeled variables constant. In other words, b reflects how sensitive a dependent measure is to changes in the independent variable. In contrast, r reflects the degree to which the z-transformed observations deviate

from any linear relationship between the two *z*-transformed variables. The *z*-transformed scores, from which the *r* statistic is derived, rely on sample standard deviations of the variables, which will vary from sample to sample. Thus, r removes information about the original units of the variables and will begin to approach the value of 1 (or −1) if changes in one variable are consistently and reliably matched to a change in the other variable (i.e., the relationship approaches linearity in *z*-transformed space). For these reasons, *b* has been recommended over *r* (which for bivariate models is equivalent to the standardized regression coefficient, *beta*) for comparisons between or among samples and for generalization to populations (Cohen, Cohen, West, & Aiken, 2003; Keith, 2006). Note that for bivariate cases within a data set, the *t*-tests of *b* and *r* against zero are equivalent and are assessed with the same degrees of freedom.

For a given participant, either statistic could be computed from the raw scores or the means of the observations associated with each level of the independent variable. The former approach would probably decrease the magnitude of *r*, but the degrees of freedom used in the *t*-test of *b* and *r* against zero would be computed from the trial total. In contrast, the latter approach would likely increase the magnitude of *r*, but the degrees of freedom would be computed from the condition total (e.g., the number of objects used). We report both variants of *r*, with the degrees of freedom differentiating the two. The two approaches would not differentially influence *b* provided there were an equivalent number of observations per level of the independent variable.

To compare patient SJ's grip scaling performance with the mean performance of the control participants, we could use *b* or *r*. But as discussed above, the use of these statistics has distinct implications. We used *r* to compare the patient's performance with the mean performance of controls (Crawford, Garthwaite, Howell, & Venneri, 2003) rather than *b*, since a comparison of a single case to a control sample using *b* requires a more stringent assumption about the distribution from which the slopes were sampled (see Crawford & Garthwaite, 2004). [Although not reported, a comparison of the *b*-statistics yielded identical conclusions.] The *r*-statistics we used to compare patient SJ's performance with the mean performance of the controls were computed for each participant separately from the means of the measurements obtained from grasping or estimating the objects.

Briefly, Crawford, Garthwaite, Howell et al. (2003) recommend a Fisher-transformation on the *r* derived from each participant. The Crawford and Howell (1998) modified *t*-test is then conducted on the transformed data (Crawford, Garthwaite, Howell et al., 2003). This modified *t*-test treats the control participants as a sample, rather than a fixed population. This method allows us to assess whether SJ's performance falls within or outside of the normally-sighted control population without inflating the per-contrast Type I error rate, α, as traditional techniques involving *z*- or *t*-statistics do (Crawford and Garthwaite, 2005b). We used a per-contrast α criterion of 0.05. Given the grip-scaling abilities of blindsight patients in the literature in their sighted and blind fields (e.g., Jackson, 1999; Perenin & Rossetti, 1996), we adopted a two-tailed criterion for the comparisons of SJ's performance in her sighted field with that of the normally-sighted controls and a one-tailed criterion for similar comparisons in her blind field given that one might expect to observe a deficit.

2.4.1. Target-localization

The principal dependent measure for the target-localization task was computed from the recorded forefinger endpoints, which were converted to a horizontal distance from the fixation cross in visual degree angle. No trials were discarded from the target-localization task. An OLS linear regression was employed to model the endpoints (in visual degree angle) for each field separately as a linear function of the distance from the fixation cross to the targets (also in visual degree angle). The regression coefficient, *b*, reported for target-localization reflects the rate of change in horizontal distance between the endpoint and the fixation cross (in degrees of visual angle) as horizontal distance between the target position and the fixation cross increases (also in degrees of visual angle).

2.4.2. Explicit target-detection

For the target-detection task, trials were removed from the analysis if patient SJ failed to respond or if her reaction time (RT) was more than 2 *SD*s larger then her mean for that condition. As a result, two trials were discarded. The analysis for the target-detection task compared patient SJ's mean RT for single-target trials which appeared in her left (sighted) visual field with the mean RT for double target trials (targets appear simultaneously in both visual fields).

2.4.3. Grasping

In-house software permitted an automated selection of movement onset, movement offset, and the principal dependent measure, peak grip aperture (PGA) for all data from the grasp session. For each sample point, grip aperture was computed as the vector distance between the IREDs located at the tip of the thumb and forefinger. The onset of the movement was defined as the first of 20 consecutive frames during which the velocity of the thumb IRED exceeded 30 mm/s. The offset of the movement was defined as the first of 20 consecutive frames during which the grip aperture velocity fell within ±30 mm/s. The movement onset and movement offset frames were used to define a search window within which the PGA was selected. Each grip aperture profile was inspected visually to ensure that there were no gross errors made in the selection of PGA. For trials where an erroneous PGA was selected, the number of consecutive frames criterion for movement offset was adjusted by increments of five.

Patient SJ committed no errors with her left hand for objects located in her left (sighted) visual field (control participants $M = 3\%$). She did, however, commit four errors (4%) with her right hand for objects located in her right (blind) visual field (control participants $M = 3\%$). These trials were discarded from the analysis and their repeats at the end of the block substituted into the analysis.

Ordinary least squares (OLS) linear regression modeled PGA on the width of the object on the current trial. The regression coefficient, *b*, for this analysis represents the rate of change in the dependent measure (in mm) per incremental increase in the width of the object (also in mm). Since there were two blocks of trials administered to test performance in the right (blind) visual field, this model was tested for the full data set and then once for each block separately.

An additional model of Session 1 PGA was tested that included the width of the object grasped on the current trial and that of the object grasped on the immediately preceding trial. The additional model, therefore, assesses whether a significant linear relationship between patient SJ's PGA (1) and the width of the current object (2) remains once the contribution of the width of the object grasped on the previous trial (3) has been partialled out of both PGA and the width of the current object. We employed this model as an additional safeguard against the possibility that SJ may intentionally or unintentionally use haptic information about the object grasped on a given trial to guide her performance on the subsequent trial. Only valid trials that were preceded by a valid trial were included in this analysis. Accordingly, the first trial of each block and each of the four error trials and their subsequent trials were discarded (total of ten). For this second model, we report the *b*-statistics and partial correlations (e.g., $r_{1.23}$). Given the nature of the trial order it was not surprising to find that the collinearity

diagnostic indicated perfect independence between the current and preceding object widths (*Tolerance* = 1.0).

3. Session 1: results

3.1. Target-localization

A linear regression of patient SJ's endpoints on the target location indicated that she was able to localize targets in both her sighted and blind fields (see Fig. 2).

Patient SJ's endpoint distance increased with the target positions located in her sighted (left) visual field ($r(29) = 0.96$, $b = 0.76$, $p < .001$; $r(2) = 0.99$) and again when the targets were located in her blind (right) visual field ($r(78) = 0.52$, $b = 0.31$, $p < .001$; $r(2) = 0.86$). Qualitatively, SJ performed this task no differently than sighted individuals would. That is to say SJ did not appear to adopt an unusual or deliberate strategy to complete this task. However, since saccade latencies were not recorded, we cannot make a formal quantitative assessment.

During the testing, patient SJ insisted that she did not see any of the targets presented in her blind field. On a few of the trials in which the target was presented 10° from the fixation cross, she remarked that she "felt" like she "saw a shadow". However, when pressed to describe the phenomenon she replied that she could derive no shape or form from the impressions. Her description suggests a type II blindsight, which reflects an awareness of a visual stimulus without a concrete description (e.g., a 'gut' feeling see Cowey, 2010). Interestingly, similar, if not identical, subjective reports like these are reported frequently in the blindsight literature (see Zeki & Ffytche, 1998).

3.2. Target-detection

Patient SJ was not reliably faster at responding to two simultaneously presented targets ($M = 349$ ms, $SD = 54$ ms) than one target ($M = 357$, $SD = 54$ ms) ($t(69) = 0.66$, $p = 0.51$). She did not respond on any of the blank 'catch' trials.

3.3. Grasping

Fig. 3 depicts patient SJ's PGA as a function of the width of the object located in her sighted (left) visual field and grasped with her left hand (panel A) and with her right hand in her blind (right) visual field (panel B).

As expected, PGA increased linearly as a function of the width of the object located in her sighted (left) field which she grasped with her left hand ($r(47) = 0.60$, $b = 0.25$, $p < 0.001$; $r(2) = 0.99$). SJ scaled her grip to the width of the object in her sighted field as reliably as the control participants, $t(11) = 0.03$, $p = 0.98$. (Fig. 3 panel C). Critically, PGA also increased linearly as a function of the width of the object located in her blind (right) field ($r(96) = 0.35$, $b = 0.17$, $p < 0.001$; $r(2) = 0.89$), although SJ's grip scaling was less reliable than that of the control participants, $t(11) = -1.98$, $p < 0.05$ (Fig. 3 panel D). Subsequent analyses of SJ's performance in her blind (right) field indicated a significant linear relationship between PGA and object width for each block separately (first block, $r(47) = 0.40$, $b = 0.21$, $p < 0.005$; second block, $r(47) = 0.30$, $b = 0.13$, $p < 0.05$).

The analysis of PGA (1) as a function of the width of the object grasped on the current trial (2) and the immediately preceding trial (3) indicated that patient SJ's PGA increased with the width of the current ($r(85)_{12.3} = 0.34$, $p < 0.001$) and previous objects ($r(85)_{13.2} = 0.41$, $p < .001$; $r(86)_{23} = 0.01$, *ns*) located in her blind (right) visual field. This suggests that both the visual information from the current object and experience with the object on the previous trial made unique and significant contributions to the programming of grip aperture for the object on the current trial. An influence of the width of the previous object was not observed when SJ grasped objects located in her sighted (left) visual field. Accordingly, SJ's PGA increased with the width of the current ($r(46)_{12.3} = 0.63$, $p < .001$) but not the width of the previous objects ($r(46)_{13.2} = 0.28$, *ns*; $r(47)_{23} = 0.10$, *ns*).

4. Session 1: discussion

The endpoints of patient SJ's pointing movements were clearly guided by the location of the targets in both her sighted (left) and blind (right) visual fields. When asked to reach out to pick up novel objects located in her blind (right) visual field with her dominant (right) hand, SJ adjusted her grip aperture with the width of the target object. Interestingly, the results of the second model that included the width of the object grasped on the previous trial indicated that SJ (either intentionally or unintentionally) used the experience gleaned from the previous trial to inform her performance on the following trial when reaching out to pick up objects located in her right (blind) but not her left (sighted) visual field. Critically, however, visual information about the width of the current object accounted for a nearly identical amount of variance in her performance on the current trial. Although the

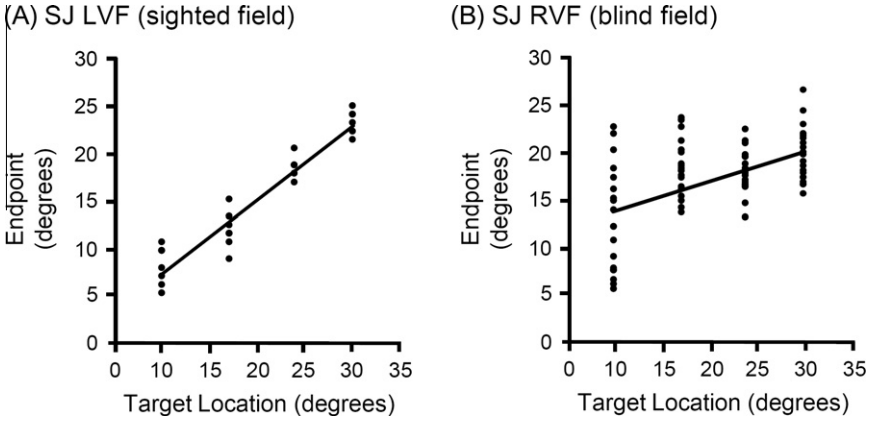

Fig. 2. Session 1 horizontal endpoint distance from the fixation cross (end-point) in visual degree angle from the fixation cross as a function of the target location (also in horizontal visual degree angle from the fixation cross) for patient SJ when pointing to targets in her left (sighted) visual field (LVF) (panel A) and in her right (blind) visual field (RVF) (panel B) with her right (dominant) hand while vision remained available throughout the movement (closed-loop feedback).

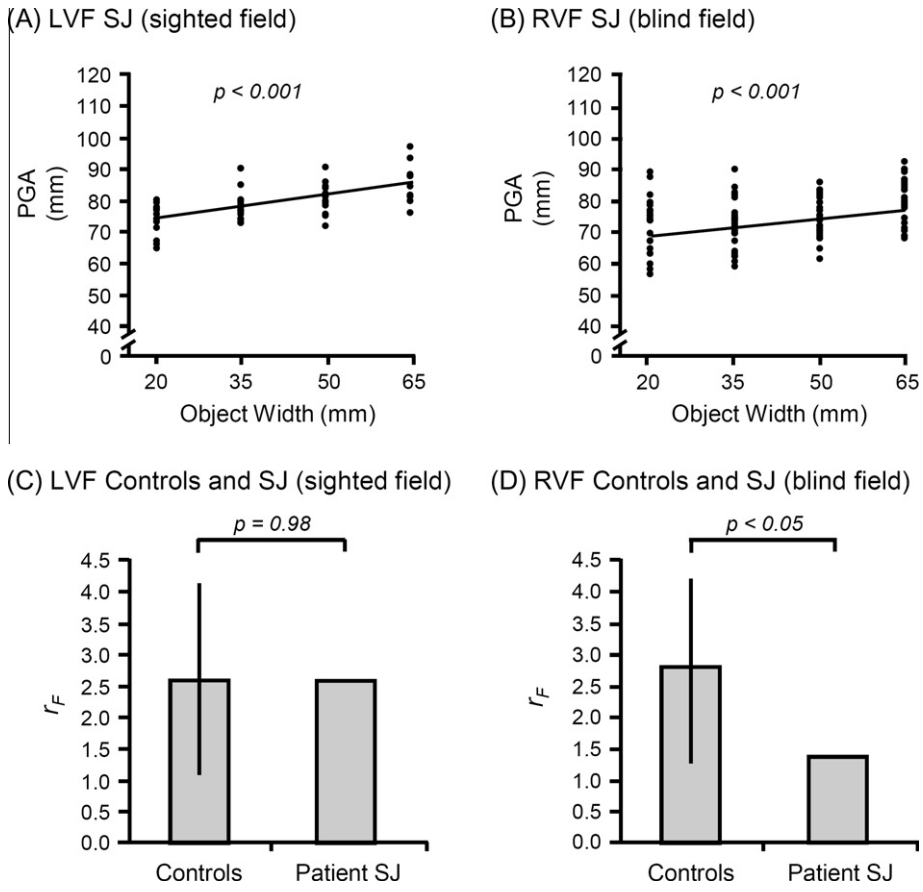

Fig. 3. Peak grip aperture (PGA) in Session 1 plotted as a function of object width for patient SJ when she grasped objects located in her sighted (left) visual field (LVF) with her left (non-dominant) hand (panel A) and in her blind (right) visual field (RVF) with her right (dominant) hand (panel B) with retinal input available during the programming and execution of the grasp (closed-loop visual feedback). Panels C and D each depict the Fisher-transformed correlation coefficient, r_F, that describes the relationship between PGA and object width for SJ and the normally-sighted control participants, who were tested under identical conditions (LVF: panel C; RVF: panel D). Solid error bars denote the 95% confidence interval around the mean r_F for control participants to compare SJ's r_F. Note that SJ showed sensitivity to the width of objects when she grasped them in both her sighted and her blind field. The reliability of SJ's grip scaling in her sighted-field (LVF) did not differ significantly from that of the control participants (panel C). The reliability of SJ's grip scaling in her blind field (RVF), however, was significantly less than that of the control participants (panel D).

slopes governing the relationship between object width and PGA appear to be similar across hands, only SJ's performance with her left hand was within the normal range. Had SJ been tested with her dominant (right) hand for both fields, a larger difference would likely have emerged between her sighted and her blind field. Nevertheless, the mean slope for grasps made into SJ's blind (right) field across the two blocks of trials ($b = 0.17$; first block, $b = 0.21$) was quite similar to the slopes we calculated from the published data on patient PJG ($b = 0.22$; Perenin & Rossetti, 1996) and patient GY ($b = 0.20$; Jackson, 1999).

At the same time, patient SJ's spared performance in these visuomotor tasks did not appear to depend on her ability to 'see' the targets or, for the purposes of grip scaling, her ability to perceive their width, shape, or form; in fact, SJ never reported seeing a target when it was presented by itself in her blind field nor was she reliably faster at responding to a target in her good field when an additional target was presented in her blind field during the target-detection task. It is important to note, however, that patient SJ's failure to show a target redundancy effect in our experiment does not mean that she is completely incapable of detecting targets in her blind field (using a button press). Had we used a forced-choice variant of this task she may have very well exhibited better-than-chance levels of performance. Furthermore, it is important to note that there is between- and within-patient variability across the range of residual visual abilities that have been tested in blindsight (e.g., Corbetta et al., 1990). Nevertheless, we found no evidence that SJ was visually conscious of any targets in her blind field even though she showed clear evidence for action blindsight.

5. Session 2: experiments

Approximately 4 months following the first session of experiments, we tested patient SJ again for replicability of our initial findings and to explore the limitations of her grip scaling in her blind field with three additional tasks. Thus, in separate testing blocks SJ grasped objects located in either her left or right visual field with (closed loop) and without (open loop) visual feedback and following a 2 s delay without feedback. In addition, as a control task, we asked SJ to manually estimate the width of the same objects presented within her sighted (left) and blind (right) visual fields. In all cases, SJ used her right hand.

5.1. Methods

5.1.1. Participants

In addition to patient SJ we tested 13 right-handed control participants ($M = 30$ years, $SD = 8$ years) 12 of whom were tested on the Session 1 grasping tasks. The control participants were tested under identical conditions as those used with SJ, but with fewer trials to keep the duration of the experiment under 2 h.

5.1.2. Experiment setup and design

The setup required few changes from those used for Session 1 grasping. A new set of four black objects was used. The object height remained the same as those used on Session 1 (1.5 cm), but the lengths were increased to 6 cm and the widths were reduced by 0.5 cm each such that the shortest object width was 1.5 cm and the longest 6 cm. The Session 2 objects were instrumented so that the time at which contact was made with the objects could be recorded electronically. Additionally, rather than keeping the location of the fixation target constant and varying the object's position as was done on Session 1 testing, the location of the fixation target varied while the location of the target object remained constant. Thus, all grasps and manual estimates were executed with the right hand while the participant fixated to the left or to the right of the object. This ensured that the biomechanical requirements for the action within each field were identical. The objects were located such that center of the edge of the object facing the participant was 30 cm from the start button. Patient SJ was seated as on Session 1. The distance from her eyes to the front edge of the object was 50 cm. The fixation points were located 10 cm from the leftmost or rightmost edge of the object. The distance, therefore, between the fixation target and the closest edge of the object subtended 11° of visual angle.

In addition to closed-loop visual feedback, we also asked patient SJ to perform grasps without visual feedback (open loop). For this condition, the trial events occurred as before, but vision was removed once the participant released the start button at the onset of the movement rather than remaining open for an additional second. Grasping was also tested in a delay condition in which vision was permitted for 1 s and the response cued 2 s thereafter by an auditory tone. All grasping tasks were administered in separate blocks of 65 trials each for patient SJ (33 trials for the control participants), while manual estimates were tested in a block of 33 trials. The trial order was constructed using the same criterion used for Session 1, except that each object was sampled 16 times for each grasping task and 8 times for manual estimations.

5.1.3. Procedure

For all tasks, the sighted (left) visual field was tested before the blind (right) visual field to further familiarize patient SJ with the requirements, and identical procedures were adopted for the 13 control participants. The starting hand configuration used for Session 1 grasps was used for grasps and manual estimates for Session 2. For the immediate grasping and manual estimation tasks, the participants were instructed to initiate their grasps when vision was permitted (i.e., when the goggles opened). For manual estimates, SJ used her forefinger and thumb to match the width of the target object without reaching towards it. Once satisfied with her estimate, she was asked to keep her fingers as stable as possible until vision was occluded by the goggles. Throughout the manual estimation task, the bottom of her hand remained rested on the table which prevented her from inadvertently directing her hand towards the object. Immediate grasping with closed-loop visual feedback was tested first, then manual estimations, followed by immediate grasping in open loop (i.e., movements without visual feedback), and then delayed grasping. As on Session 1, trials during which SJ appeared to move her eyes, fumbled the object, or initiated her movement too early were noted and repeated at the end of the block.

5.1.4. Data processing and statistical analysis

For all tasks, movement onset corresponded to the sample frame at which the start button was released. For the grasping tasks, movement offset corresponded to the sample frame at which the contact was made with either the front or back side of the target object. Grip aperture and PGA were defined as on Session 1. The principal dependent measure for manual estimation was the manual estimate aperture (MEA) which was defined as the first of 30 consecutive frames following movement onset during which the speed at which the thumb and finger closed or opened fell below 30 mm/s. This threshold reflected a point at which the grip aperture remained highly stable and was thought to best represent the participant's estimate of the object's width given the experimenter's instruction to preserve their estimate until vision was occluded.

The data were analyzed using the first model employed for Session 1 grasps, which described PGA as an OLS determined linear function of the width of the object grasped on the current trial. For grasps executed with closed-loop visual feedback, patient SJ committed seven errors in her sighted (left) visual field (11%) and five in her blind (right) visual field (8%); for comparison, the average error rate for the control participants was 7% for each field. For grasps executed without visual feedback (open loop), SJ committed one error in her sighted (left) field (2%) and two errors in her blind (right) field (3%); for comparison, the average error rate for the control participants was 3% for each field. Finally, for delayed grasps, SJ committed two errors in her sighted field (4%) and three errors in her blind field (5%); for comparison, the average error rate for the control participants was 7% for the left and 3% for the right visual fields. As on Session 1, all error trials were discarded from the analysis and the missing values replaced with the data from the corresponding trials that were repeated at the end of the block.

In addition to comparing patient SJ's performance against the mean performance of the normally-sighted control participants, we examined whether SJ's grip-scaling deficits in delayed and manual matching tasks dissociated from her performance in the immediate 'real-time' grasping task. To this end, we adopted Crawford, Garthwaite, and Gray's (2003) criterion for dissociation. We expected that SJ's performance on real-time grasping in her blind field would differ from her performance on delayed grasping or manual estimation more than similar contrasts in the normally-sighted controls. Additionally, SJ's performance on at least one of these tests should dissociate from the mean performance of the controls. This was formally tested using Crawford and Garthwaite's (2005a) revised standardized difference test (see also Crawford & Garthwaite, 2005b). As was the case for the Session 1 results, the per-contrast α criterion was 0.05, with a one-tailed criterion set for the comparisons between SJ and the controls for performance in the blind (right) visual field and a two-tailed criterion set for the comparisons between SJ and the controls for performance in the sighted (left) visual field. Finally, although a one-tailed test would be justified, we adopted the more conservative two-tailed criterion to assess whether the reliability of SJ's grip scaling to objects located in her blind field in immediate grasping dissociated from her performance in the same field for delayed grasping and manual estimation.

5.2. Results

5.2.1. Immediate grasping with visual feedback (closed loop)

Similar to the results of Session 1 testing, patient SJ's PGA increased with the width of objects located in her sighted (left) field ($r(63) = 0.72$, $b = 0.39$, $p < 0.001$; $r(2) = 0.99$). SJ's grip scaling in her sighted field was as reliable as that observed in the normally-sighted controls, $t(12) = 0.06$, $p = 0.95$. (see Fig. 4: panels A and C).

Critically, SJ's PGA increased with the width of objects located in her blind (right) field ($r(63) = 0.33$, $b = 0.14$, $p < 0.01$; $r(2) = 0.95$). However, similar to the results of Session 1, SJ's grip scaling to the width of objects located in her blind field was less reliable than that of the control participants, $t(12) = -2.30$, $p < 0.05$ (see Fig. 4: panels B and D).

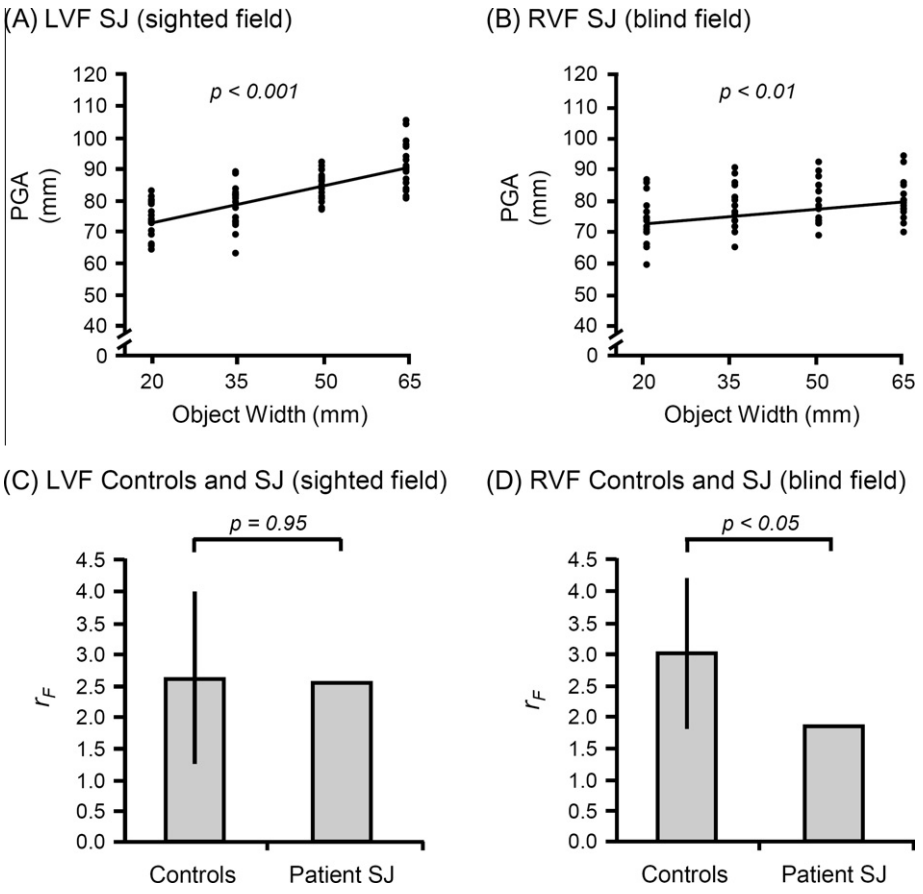

Fig. 4. Peak grip aperture (PGA) in Session 2 plotted as a function of object width for patient SJ when she grasped objects located in her sighted (left) visual field (LVF) (panel A) and in her blind (right) visual field (RVF) (panel B) with her right (dominant) hand with retinal input available during the programming and execution of the grasp (closed-loop visual feedback). Panels C and D each depict the Fisher-transformed correlation coefficient, r_F, that describes the relationship between PGA and object width for SJ and the normally-sighted control participants, who were tested under identical conditions (LVF: panel C; RVF: panel D). Solid error bars denote the 95% confidence interval around the mean r_F for control participants to compare SJ's r_F. Similar to what happened in Session 1, SJ showed sensitivity to the width of objects when she grasped them in both her sighted and her blind field. The reliability of SJ's grip scaling in her sighted-field (LVF) did not differ significantly from that of the control participants (panel C). The reliability of SJ's grip scaling in her blind field (RVF), however, was significantly less than that of the control participants (panel D).

5.2.2. Immediate grasping without visual feedback (open loop)

In general, patient SJ's performance when grasping without visual feedback (i.e., in open loop) resembled her performance with closed-loop feedback. Accordingly, her PGA increased with the width of objects located in her sighted (left) ($r(63) = 0.74$, $b = 0.35$, $p < 0.001$; $r(2) = 0.98$), and she scaled her grip to the width of the object as reliably as the control participants, $t(12) = -0.45$, $p = 0.66$ (see Fig. 5: panels A and C).

Critically, SJ's PGA increased with the width of objects located in her blind (right) field ($r(63) = 0.26$, $b = 0.12$, $p < 0.05$; $r(2) = 0.95$). However, SJ's grip scaling to the width of objects located in her blind field was less reliable than that of the control participants, $t(12) = -1.73$, $p = 0.05$ (see Fig. 5; panels B and D).

5.2.3. Delayed grasping

Consistent with the results from immediate grasping, when patient SJ grasped objects following a delay, her PGA increased with the width of objects presented in her sighted (left) visual field ($r(63) = 0.51$, $b = 0.30$, $p < .001$; $r(2) = 0.99$), and she scaled her grip to the width of the object as reliably as the control participants, $t(12) = 1.86$, $p = 0.09$ (see Fig. 6: panels A and C).

The results were quite different for the blind field. In striking contrast to her results from the immediate grasping conditions, SJ's PGA in the delay condition showed no sensitivity to the width of objects presented in her blind (right) field ($r(63) = -0.11$, $b = -0.04$, $p = 0.38$; $r(2) = -0.63$). Not surprisingly, therefore, the reliability of SJ's grip scaling in her blind field differed significantly from that observed in the normally-sighted control participants, $t(12) = -4.53$, $p < 0.001$ (see Fig. 6: panels B and D). The results of the dissociation analysis indicated that the reliability of SJ's grip scaling to objects located in her blind field in both the immediate ($t(12) = -2.71$, $p < .01$) and the delayed grasping conditions ($t(12) = -6.63$, $p < .001$) was significantly poorer than it was in the normally-sighted controls. But the difference in the reliability of SJ's grip scaling between the immediate and the delayed condition in her blind field was significantly greater than the corresponding difference for the normally-sighted controls, $t(12) = 3.09$, $p < .01$. The same comparison for SJ's immediate and delayed grasping in her sighted field yielded no evidence that her performance declined with delay. That is, although SJ performed worse overall than controls when grasping in her blind field, the significant decrease in the reliability of grip scaling in the delay condition for SJ was much greater than the same decrease in performance observed in the control group. To put it plainly, the introduction of a 2 s delay had a much greater impact on SJ's performance compared to controls.

5.2.4. Immediate manual estimation with visual feedback (closed loop)

The pattern of results observed for manual estimation was similar to that observed with delayed grasping. In her sighted (left) visual field, patient SJ's MEA increased with object width ($r(31) = 0.84$, $b = 0.99$, $p < .001$) (see Fig. 7: panel A). SJ's grip scaling

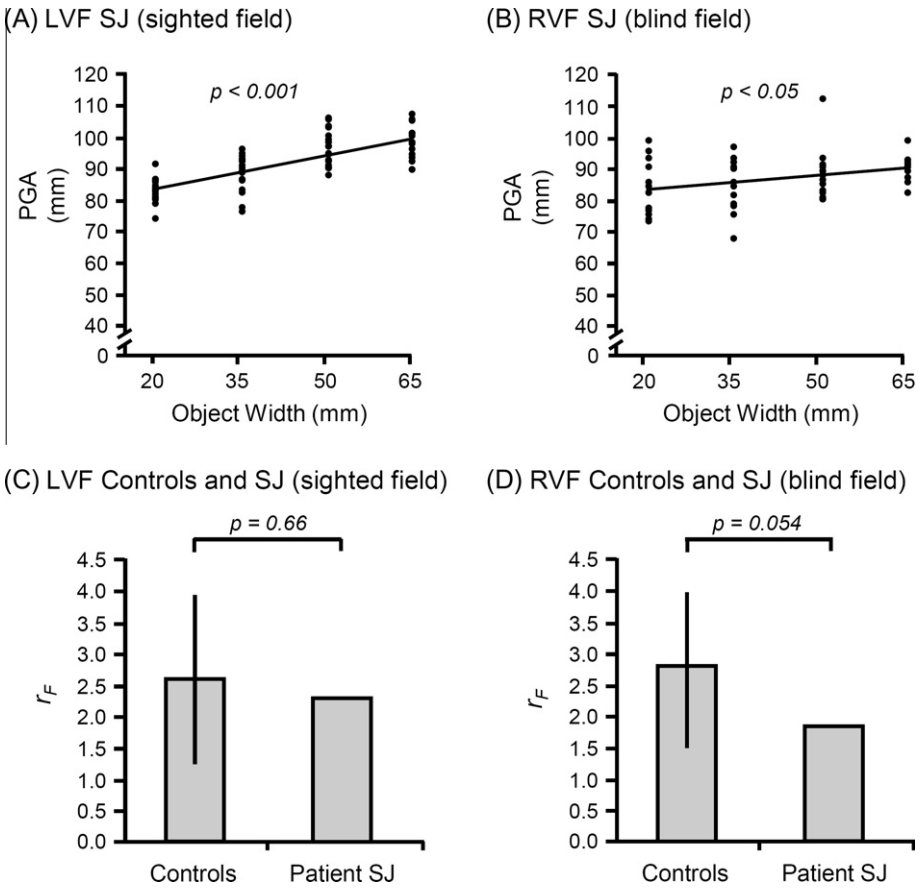

Fig. 5. Peak grip aperture (PGA) in Session 2 plotted as a function of object width for patient SJ when grasping objects located in her sighted (left) visual field (LVF) (panel A) and blind (right) visual field (RVF) (panel B) with her right (dominant) hand with retinal input available during the programming but not the execution of the grasp (open-loop visual feedback). Panels C and D each depict the Fisher-transformed correlation coefficient, r_F, that describes the relationship between PGA and object width for SJ and the normally-sighted control participants, who were tested under identical conditions (LVF: panel C; RVF: panel D). Solid error bars denote the 95% confidence interval around the mean r_F for control participants to compare SJ's r_F. Again, similar to what happened in Session 1, SJ showed sensitivity to the width of objects when she grasped them in both her sighted and her blind field. The reliability of SJ's grip scaling in her sighted-field (LVF) did not differ significantly from that of the control participants (panel C). The reliability of SJ's grip scaling in her blind field (RVF), however, was significantly less than that of the control participants (panel D).

when manually matching the width of the objects located in her sighted field was as reliable as that observed in the normally-sighted controls, $t(12) = 1.09$, $p = 0.30$ (see Fig. 7: panel C).

In her blind (left) field, however, her MEA showed no sensitivity to object width ($r(31) = -0.08$, $b = -0.11$, $p = 0.66$; $r(2) = -0.53$) (see Fig. 7: panel B). Thus, it was hardly surprising to find that the reliability of SJ's grip scaling to the widths of objects located in her blind field was significantly poorer than it was for grip scaling in the control participants ($t(12) = -5.63$, $p < 0.001$), who had no trouble indicating the width of the objects (see Fig. 7: panel D). The results of the dissociation analysis indicated that the reliability of SJ's manual estimation of the width of objects located in her blind field was significantly poorer than it was for manual estimations made by the normally-sighted controls, $t(12) = -9.06$, $p < .001$. But the difference in the reliability of SJ's grip scaling between the immediate grasping and manual estimates in her blind field was significantly greater than the corresponding difference in the normally-sighted controls, $t(12) = 4.61$, $p < 0.001$. The same comparison with respect to controls for SJ's immediate grasping and manual estimates in her sighted field yielded no significant differences.

5.3. Discussion

In agreement with Perenin and Rosseti's (1996) findings, the results of Session 2 show that even though patient SJ was unable to report the size of an object in her blind (right) field by using a manual estimate, her grip aperture remained sensitive to the width of that object when she reached out to pick it up. Furthermore, the results from Session 2 show that her ability to scale her grip to the width of objects in her blind field was not entirely dependent on having vision available during the movement; SJ continued to scale her grip even when vision was removed at movement onset (open loop). Importantly, however, SJ's sensitivity to object width deteriorated dramatically when she was cued to reach out and pick up the object in her blind field only 2 s after vision of her hand and the object was removed. Thus, the critical factor appears to be whether or not vision was available during the programming of the grasping movement.

Even though patient SJ showed evidence for grip scaling to object width in her blind (right) field, her scaling was not as sensitive as that of our normally-sighted control participants. This suggests that, in the intact brain, V1 must make some contribution to the visuomotor networks mediating grasping. The fact that SJ performed as well in her sighted (left) visual field as control participants suggests that she does not possess a global deficit in grip scaling.

The preserved grip scaling in SJ's blind field raises the question as to how retinal input from that blind field is reaching the visuomotor networks, presumably in the dorsal stream, that are controlling this behavior. In the final Session of testing we used fMRI to see if area MT, one of the possible routes into the dorsal stream,

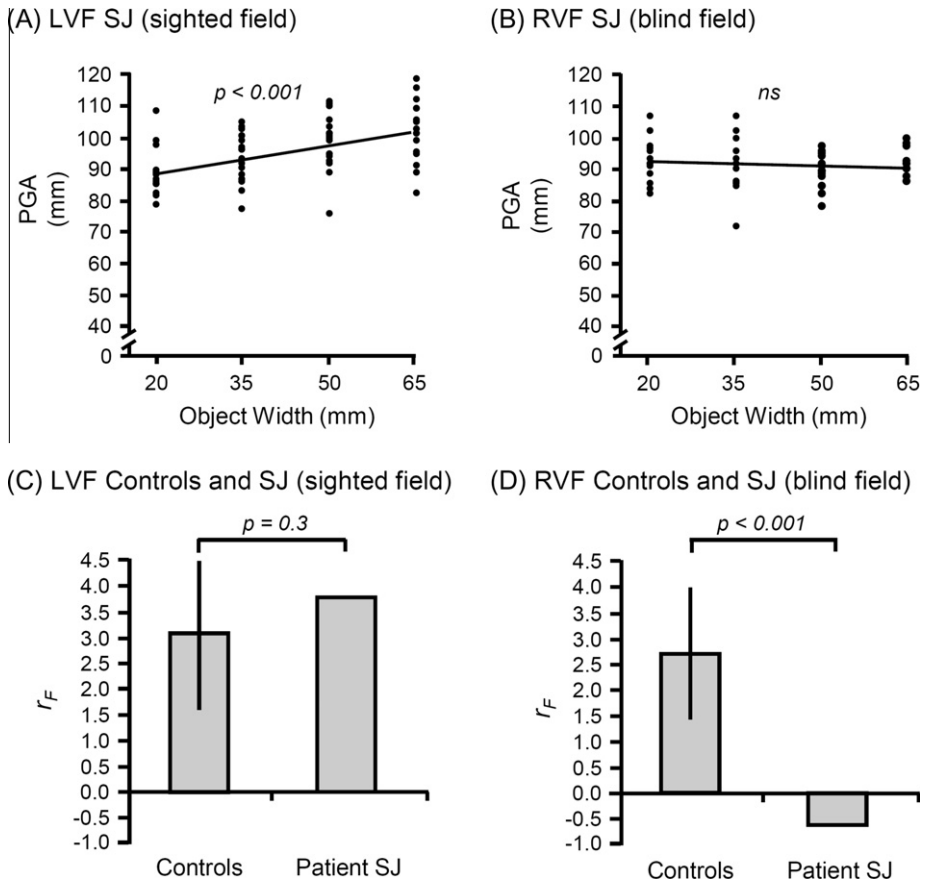

Fig. 6. Peak grip aperture (PGA) in Session 2 plotted as a function of object width for patient SJ when she was cued to grasp objects located in the left visual field (LVF) (panel A) and right visual field (RVF) (panel B) with her right (dominant) and 2 s after a 1 s preview of the object. Thus, retinal input was not available for either the programming or execution of the grasp (delayed grasping). Panels C and D each depict the Fisher-transformed correlation coefficient, r_F, that describes the relationship between PGA and object width for SJ and the normally-sighted control participants, who were tested under identical conditions (LVF: panel C; RVF: panel D). Solid error bars denote the 95% confidence interval around the mean r_F for control participants to compare SJ's r_F. Unlike her performance when retinal input was available during the programming of the grasp, SJ's PGA is sensitive to the width of objects only when they are located in her sighted field and not when they are located in her blind field. Critically, the reliability of SJ's grip scaling in her sighted-field (LVF) did not differ significantly from that of the control participants (panel C). The reliability of SJ's grip scaling in her blind field (RVF), however, was significantly less than that of the control participants (panel D).

was still functioning in SJ's damaged hemisphere, despite the large lesion in V1.

6. Session 3: experiment

Approximately 5 months following Session 2 testing, we brought patient SJ back for an MRI session to acquire high-resolution anatomical images and measure blood oxygen-level dependent (BOLD) signaling related to moving stimuli in her blind and sighted visual fields. Our aim was to test whether or not our visual stimulus would invoke BOLD signaling in SJ's intact extrastriate regions, particularly for moving stimuli presented in her blind field – and to see if there was any spared tissue around the V1 lesion that would respond accordingly.

6.1. Methods

6.1.1. Data acquisition and analysis

The MRI data were collected on a 3 Tesla Siemens Tim-Trio MRI scanner at the Robarts Research Institute (London, Ontario) using a 32-channel head coil. To collect functional data we used a T2* weighted single shot EPI imaging sequence (TR = 2 s, TE = 30 ms, 36 slices, 3 mm iso-voxels, flip angle 90°, in-place resolution 80×80, FOV = 240×240). The functional data were aligned to a high resolution (1 mm iso-voxel) 192 slice T1 anatomical scan.

The stimuli used during the MT+/V5 localizer scans were displayed on a 15×20 cm screen using an LCD projector (AVOTEC Silent Vision Model 6011). Patient SJ viewed the stimuli on a screen through a front surface mirror mounted on top of the head coil and was instructed to fixate on a red dot (0.5°) presented at the center of the screen. An MR-compatible infrared camera was used to monitor her eye movements 'online'. Each scan began with the first of nine blocks of 16 s of baseline stimuli, which were interleaved with eight blocks of 16 s of motion stimuli. The baseline stimuli consisted of a pseudo-random pattern of white dots (diameter 0.1° visual angle and spaced, on average, 1° of visual angle apart) that flickered at 1 Hz against a black background. The motion stimuli consisted of the same pattern of white dots translating coherently across the visual field in a random direction. The direction of the moving dots was randomly changed every second. The sighted and blind fields were tested in separate scans of 136 volumes (approximately 4 min 30 s) each.

Data were analyzed using BrainVoyager QX 2.1 (Brain Innovation, Maastricht, The Netherlands). The data were preprocessed prior to the statistical analysis. First, the scans were slice scan time corrected using a cubic-spline interpolation. Next, the volumes for each functional scan were transformed to coincide spatially with the first volume of the scan closest to the high-resolution

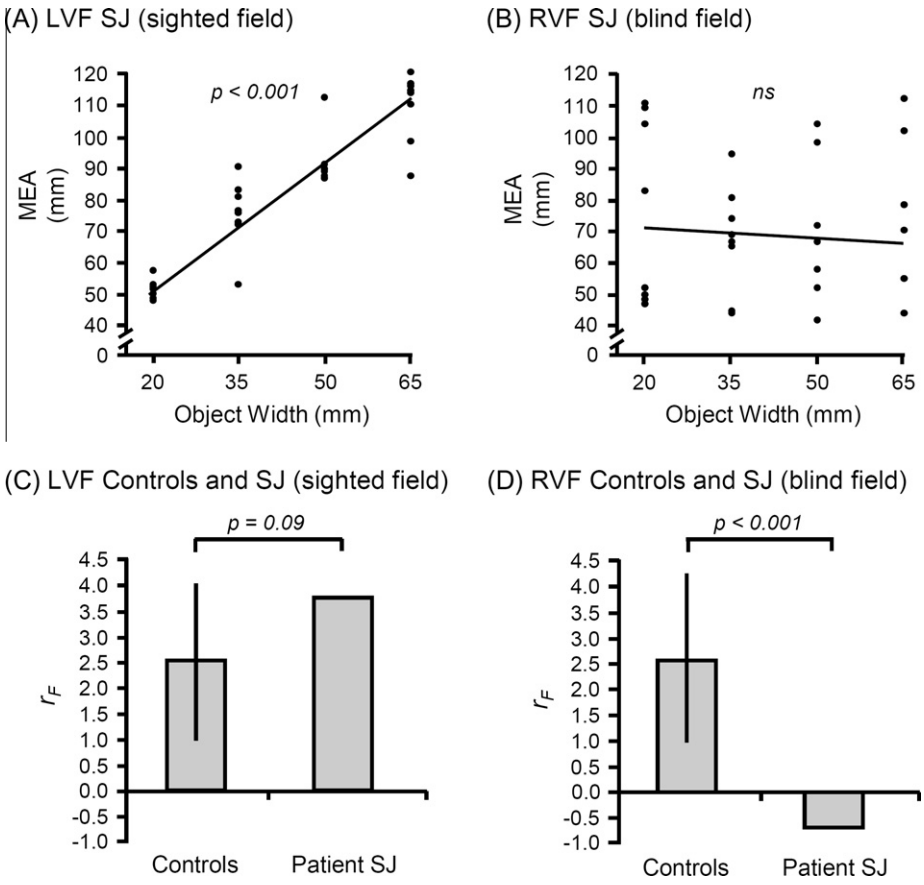

Fig. 7. Manual estimate aperture (MEA) in Session 2 plotted as a function of object width for patient SJ when she used her forefinger and thumb to manually match the width of objects located in her sighted (left) visual field (LVF) (panel A) and right visual field (RVF) (panel B) without reaching towards the object and when retinal input was available during the programming and execution of the manual estimate (closed-loop visual feedback). Panels C and D each depict the Fisher-transformed correlation coefficient, r_F, that describes the relationship between MEA and object width for SJ and the normally-sighted control participants, who were tested under identical conditions (LVF: panel C; RVF: panel D). Solid error bars denote the 95% confidence interval around the mean r_F for control participants to compare SJ's r_F. Similar to her performance with delayed grasping, SJ's MEA is sensitive to the width of objects located in her sighted field but not when they are located in her blind field. Critically, the reliability of SJ's manual estimates in her sighted-field (LVF) did not differ significantly from that of the control participants (panel C). The reliability of SJ's manual estimates in her blind field (RVF), however, was significantly less than that of the control participants (panel D).

anatomical scan using the trilinear-sync correction method. This method uses a trilinear nearest neighbor algorithm to detect spatial discrepancies between temporally adjacent volumes and a sync-interpolative method to estimate the required transformation with three rotation and three translation parameters. Finally, each scan was temporally high-pass filtered by regressing the BOLD time course using a Fourier basis set composed of two sine and cosine functions and a linear component. No spatial smoothing kernel was applied to the data.

Statistical analysis was conducted separately for each scan using multiple regression of the percent transformed signal on the convolved 'predictor of interest' for motion (scaled to one) and six 'predictors of no interest' corresponding to the time course of the six motion parameter estimates derived from the preprocessing step mentioned above (see e.g., Johnstone et al., 2006). The dependent measure for statistical analysis is the unstandardized regression coefficient for the motion stimuli (β_{motion}) and represents the average measured rate of change in percent BOLD per expected incremental increase in BOLD while all other predictors are held constant. The resultant statistical map (activation) reflect the *t*-statistic returned from the test of β_{motion} against zero and was thresholded using a cluster extent determined using an extension of the Forman et al. (1995) Monte Carlo method (see Goebel, Esposito, & Formisano, 2006) with the cluster-level per-family error rate (α) held to 0.01 or less.

6.2. Results

As can be seen in Figs. 8a and 9a, moving stimuli presented in SJ's sighted (left) visual field elicited functional activation in and around intact cortical tissue forming the calcarine sulcus (i.e., striate cortex V1) of SJ's right hemisphere.

In contrast, moving stimuli presented to SJ's blind (right) visual field failed to invoke activation in any of the grey matter immediately surrounding SJ's lesion in her left hemisphere (see Figs. 8b and 9b), even at an uncorrected threshold of $p < .01$ (Stoerig, Kleinschmidt, & Frahm, 1998). Thus, the vascular response and underlying metabolic activity of the remaining portion of cortex at patient SJ's occipital pole is not influenced by moving stimuli. This result does not lend support to Campion, Latto, and Smith's (1983) suggestion (see also Fendrich, Wessinger, & Gazzaniga, 1992) that spared areas of V1 mediate blindsight.

Regions beyond the calcarine sulcus, however, showed robust activation in response to moving stimuli presented in either the blind (left) or sighted (right) visual fields (see Fig. 10a and b, respectively).

Bilateral activation was found in motion-sensitive extrastriate regions corresponding to the middle temporal and superior temporal gyri (MT+/V5 and STS, respectively). Moving stimuli presented in SJ's sighted (left) or blind (right) visual field invoked bilateral activation in the motion-sensitive areas MT+/V5 and STS of the

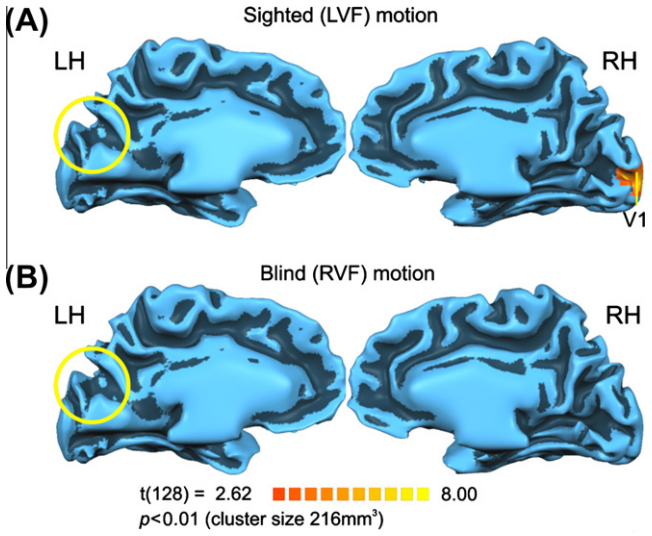

Fig. 8. Medial view of Session 3 functional imaging MT + localizer data for patient SJ when the moving visual stimulus was presented in the sighted (left) (panel A) or blind (right) visual field (panel B). The data are displayed on a segmented and smoothed version of SJ's brain to allow an extensive view of the sulci (dark blue) and gyri (light blue). The yellow circles depict the site of SJ's occipital lesion. Abbreviations: LH = left hemisphere, RH = right hemisphere, LVF = left visual field, RVF = right visual field, V1 = primary visual cortex. Note the absence of any activation in V1 in the damaged (left) hemisphere when the motion stimulus was presented within her blind (right) visual field. In comparison, the same stimulus presented within her sighted (left) visual field resulted in robust V1 activation in the normal (right) hemisphere.

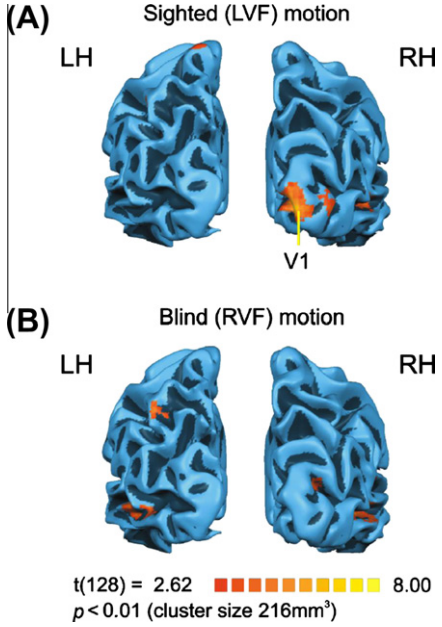

Fig. 9. Posterior view of Session 3 functional imaging MT + localizer data for patient SJ when the moving visual stimulus was presented in the sighted (left) (top panel A) or blind (right) visual field (bottom panel B). The data are displayed on a segmented and smoothed version of SJ's brain to allow an extensive view of the sulci (dark blue) and gyri (light blue). Abbreviations: LH = left hemisphere, RH = right hemisphere, LVF = left visual field, RVF = right visual field, V1 = primary visual cortex. Note the lack of significant activity in and around the left occipital pole for visual stimuli presented in SJ's blind (right) visual field.

right hemisphere (see Fig. 10) (Culham, He, Dukelow, & Verstraten, 2001; Dukelow et al., 2001; Watson et al., 1993). The results are consistent with SJ's subjective descriptions of her ability to sense

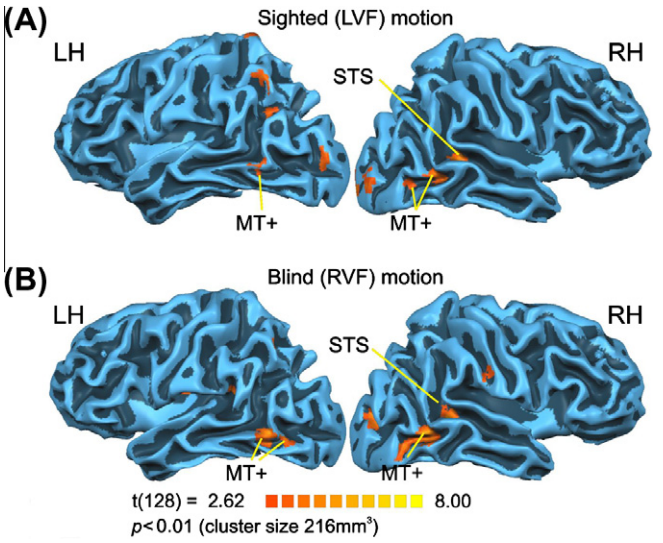

Fig. 10. Lateral view of Session 3 functional imaging MT + localizer data for patient SJ when the moving visual stimulus was presented in the sighted (left) (top panel A) or blind (right) visual field (bottom panel B). The data are displayed on a segmented and smoothed version of SJ's brain to allow an extensive view of the sulci (dark blue) and gyri (light blue). Abbreviations: LH = left hemisphere, RH = right hemisphere, LVF = left visual field, RVF = right visual field, MT+ = middle-temporal cortex, STS = superior temporal sulcus. Note the significant bilateral activation in the motion-sensitive complex MT + regardless of whether the motion stimulus appeared within SJ's sighted (left) or blind (right) visual field. Also note the lack of activation at the occipital pole of SJ's left hemisphere.

that things are moving within her blind visual field. Indeed, at the end of the experiment SJ mentioned that on some occasions she felt like something was moving in her blind field; however, she could not "see" it. These results are also consistent with previous work which demonstrated that BOLD signaling in extrastriate regions can be modulated by moving stimuli presented in the blind field of patient GY (Goebel, Muckli, Zanella, Singer, & Stoerig, 2001; Zeki & Ffytche, 1998).

6.3. Discussion

On Session 3, patient SJ was brought back for an fMRI experiment to measure how her intact and lesioned visual cortices would respond to moving stimuli presented in her sighted and blind visual fields. The results were clear. Not surprisingly, moving stimuli located in SJ's sighted (left) visual field increased BOLD signaling in the cortex surrounding the calcarine sulcus and in the expected extrastriate regions of visual cortex, namely MT+ in both hemispheres. Critically, moving stimuli presented in SJ's blind (right) visual field failed to modulate BOLD signaling in the cortical tissue surrounding SJ's lesion in the calcarine cortex yet these same stimuli elicited a robust response bilaterally in MT+. These findings raise the possibility that SJ's spared visuomotor abilities could be mediated by these intact extrastriate pathways.

In addition, the fact that MT+ is activated by moving stimuli in SJ's blind field may explain why she is sometimes able to sense that things are moving within her blind visual field. Indeed, at the end of the fMRI experiment SJ mentioned that on some occasions she felt like something was moving in her blind field but that she could not "see" it. Overall, these results resonate with previous neuroimaging work showing that neurovascular responses in extrastriate regions including MT+ can be modulated by moving stimuli restricted to the blind field of patients with hemianopia (Barbur, Watson, Frackowiak, & Zeki, 1993; Baseler, Morland, & Wandell, 1999; Goebel et al., 2001; Watson et al., 1993; Zeki & Ffytche, 1998).

7. Conclusion

The fact that SJ could scale her grasp to the width of unseen objects in her blind field suggests that neither conscious vision nor input from V1 is required for grip scaling. In addition, the fact that she could do this even when vision was removed at movement onset shows that the visuomotor networks mediating this spared ability can generate reliably scaled grasping without visually-driven 'online' control. It is important to emphasize, however, that grip scaling in SJ's blind field was still impaired compared to grip scaling in the normally-sighted control participants. But in fact this finding is quite consistent with similar findings in a number of previous investigations showing that patients with V1 lesions have relatively shallow grip-scaling slopes in their blind field (e.g., Jackson, 1999; Perenin & Rossetti, 1996). Nevertheless, even though this suggests that V1 contributes a good deal of sensitivity to the programming of grasping, it is clear that grip scaling can occur in its absence.

Perhaps the most interesting finding in the current set of experiments is the fact that SJ could not scale her grip aperture to the width of objects presented in her blind field when a 2 s delay was introduced prior to the cue to respond. These findings resonate with recent observations of patient CB who also developed a profound hemianopia following a V1 lesion (Striemer et al., 2009). Despite his lesion, CB was able to avoid unseen obstacles presented in his blind field in real-time but failed to do so if vision was removed 2 s before the cue to reach was presented. Taken together, the current study and the earlier work with CB provide converging evidence that the inputs to the visuomotor networks mediating these abilities operate optimally in real-time using information immediately available on the retina (Milner & Goodale, 2006).

There is good reason to believe that the visuomotor networks mediating spared abilities in patients like SJ and CB with action blindsight reside in the dorsal visual stream (Milner & Goodale, 2006). But how is information conveyed to these networks in the absence of V1? One candidate pathway involves area MT, which is known to project to areas in the posterior parietal cortex including the intra-parietal sulcus and the parietal–occipital cortex (Blatt, Andersen, & Stoner, 1990; Galletti et al., 2001; Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986) that have been implicated in visuomotor control (for review see; Born & Bradley, 2005; Culham, Cavina-Pratesi, & Singhal, 2006). As we reviewed in the Introduction (Section 1), there is evidence in non-human primates that visual input can reach area MT via projections from the pulvinar, a nucleus in the thalamus that has been shown to receive input from the superior colliculus (Berman & Wurtz, 2010, 2011; Kaas & Lyon, 2007; Lyon, Nassi, & Callaway, 2010) or even directly from the retina (Warner et al., 2010). In addition, there is evidence for projections to MT and other extrastriate regions from the interlaminar layers of the dLGN (Sincich et al., 2004; Vakalopoulos, 2005) and these projections have been shown to be critical for at least some residual visually guided behavior after V1 lesions (Schmid et al., 2010). Overall, these findings indicate that the dorsal stream retains some access to bottom-up retinal input in the absence of V1. [Of course, the ventral stream almost certainly has access to visual inputs that bypass V1 as well (for a discussion of this issue, see Milner & Goodale, 2006).]

The fact that patient SJ shows activation in area MT+ when viewing moving visual stimuli presented in her blind field shows that input from the retina could potentially reach dorsal-stream structures implicated in visuomotor control without involving V1. One has to be cautious in making this inference, however, because we have not demonstrated directly that visuomotor areas in the dorsal stream are activated when SJ reaches out to grasp objects in her blind field. Nevertheless, the robust activation in area MT+ from unseen visual stimuli coupled with the absence of activation in the tissue immediately adjacent to the lesion in the calcarine sulcus of her damaged hemisphere, certainly suggests that the dorsal stream could retain access to the information necessary for the visual control of grasping and other visually guided actions in the absence of V1.

Importantly, the visually-guided grasping that survives V1 damage in SJ is limited to real-time. In other words, she can scale her grasp to unseen objects in her blind field only when they are present on her retina. When a delay was introduced between last viewing the object in her blind field and initiating the grasp, she no longer showed any evidence of scaling. It has been suggested that delayed grasping is driven by visual memories of the target object that are dependent on previous perceptual processing by the ventral stream (Goodale, Jakobson, & Keillor, 1994; Goodale, Meenan et al., 1994). In other words, one has to perceive an object in the first place in order to grasp it after a delay when that object is no longer visible. Certainly, there is no evidence that SJ perceived the target objects in her blind field. Indeed, throughout both testing days SJ repeatedly insisted that she "saw nothing" in her blind field. These claims were further validated by the fact that SJ was unable to manually estimate the size of the target objects when they were presented within her blind field. The fact that SJ could scale her grasp in real-time but not after a delay is consistent with Milner and Goodale's (2006) contention that the dorsal stream does not store visuomotor transformations for later use, but rather, computes them on demand depending on current task requirements. According to their account, it is the ventral stream that mediates actions based on past visual input. SJ's failure to perceive objects in her blind field and the absence of grip scaling in delayed grasping suggests that perceptual processing in the ventral stream (at least for explicit tasks) depends on V1. Taken together then, SJ's pattern of spared visuomotor abilities and perceptual deficits fits well with Milner and Goodale's perception and action model.

There are a number of remaining questions that need to be addressed in future investigations. First, to what extent can the dorsal stream stripped of its V1 input extract the necessary information to grasp more complex objects that have constrained grasp points (e.g., the "Blake shapes"). Second, how 'real-time' is the processing in the dorsal stream without V1? In other words, would delays of less than 2 s allow some grip scaling to take place (e.g., Westwood & Goodale, 2003)? Finally, it will also be important for future studies to try and further delineate the brain regions and visual pathways that subserve action blindsight using functional brain imaging and diffusion tensor imaging, similar to recent efforts that have examined the possible neural substrates of spatial summation, pupillary responses, and other visual abilities that survive damage to primary visual cortex (Leh, Johansen-Berg et al., 2006; Leh et al., 2009; Tamietto et al., 2010).

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