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Christopher L. Striemer, Craig S. Chapman, Melvyn A. Goodale

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The role of non-conscious visual processing in obstacle avoidance: A commentary on Ross et al. (2018)

Christopher L. Striemer [a,b,*], *Craig S. Chapman* [b,c] *and Melvyn A. Goodale* [d]

[a] *Department of Psychology, MacEwan University, Edmonton, Alberta, Canada*
[b] *Neuroscience and Mental Health Institute, University of Alberta, Edmonton, Alberta, Canada*
[c] *Department of Physical Education and Recreation, University of Alberta, Edmonton, Alberta, Canada*
[d] *Brain and Mind Institute, University of Western Ontario, London, Ontario, Canada*

In 2009 we published a study in which a patient (C.B.) with damage to his right occipital lobe showed sensitivity to the position of unseen obstacles placed in his blind (left) visual field (Striemer, Chapman, & Goodale, 2009). That is, C.B.'s reach trajectory deviated away from the obstacle more when it was closer to his reaching hand, compared to when it was further away from his reaching hand (Fig. 1). In a follow-up experiment in the same paper we demonstrated, following a 2-sec memory delay, that the patient's sensitivity to the position of these unseen obstacles disappeared. It is important to emphasize that, throughout both experiments, C.B. was never aware of any obstacles in his blind field, and he never collided with a single object in his blind field. Based on these data we concluded that the dorsal visual pathway operates in real-time on a moment-to-moment basis. Furthermore, we suggested that the subcortical visual pathways that are thought to be responsible for action blindsight are capable of providing the dorsal stream with enough information to perform relatively complex visuomotor tasks like obstacle avoidance.

In a recent study published in *Cortex* Ross and colleagues (Ross, Schenk, Billino, Macleod, & Hesse, 2018) present data from six patients with visual field defects (either hemianopia or quadrantanopia) in which they failed to find any evidence of obstacle avoidance in any of their patients' blind fields. Essentially, they failed to replicate our earlier 2009 findings. Based on these null findings, Ross and colleagues conclude that, "…behavior in complex visuomotor tasks relies on input from occipital areas (abstract)" and, "there is currently no compelling neuropsychological evidence supporting the suggestion that V1-input is less relevant for dorsal than for ventral stream functions (p. 25)." In fact, based on their data Ross et al. (2018) went as far as suggesting that, "…it cannot be excluded that the observations reported by Striemer, Chapman, et al. (2009) may simply reflect a chance finding (p. 23)."

When summed together Ross et al.'s (2018) data and conclusions appear not only to be a clear failure to replicate, but call into question the validity of our original result by labelling it a "chance finding". Typically, bold statements such as these need to be backed up by firm conclusive data. In the following commentary, we provide a critical analysis of Ross et al.'s (2018) findings. We believe that a close examination of their study casts serious doubt on the validity and relevance of their bold claims. Specifically, we address what we believe is their misguided motivation for undertaking the study, and discuss several critical methodological limitations that almost certainly ensured that they would find the null-effect their entire argument hinges upon. Indeed, we suggest that Ross et al.'s (2018) findings could actually be interpreted as indirect support for our original claims.

1. Setting up the straw-man

In their Introduction Ross et al. (2018) make several bold statements that are based on what we think is a misinterpretation of our previous work. By doing so, they bolstered the

* *Corresponding author*. Department of Psychology, MacEwan University, Edmonton, Alberta, Canada.
E-mail address: striemerc@macewan.ca (C.L. Striemer).
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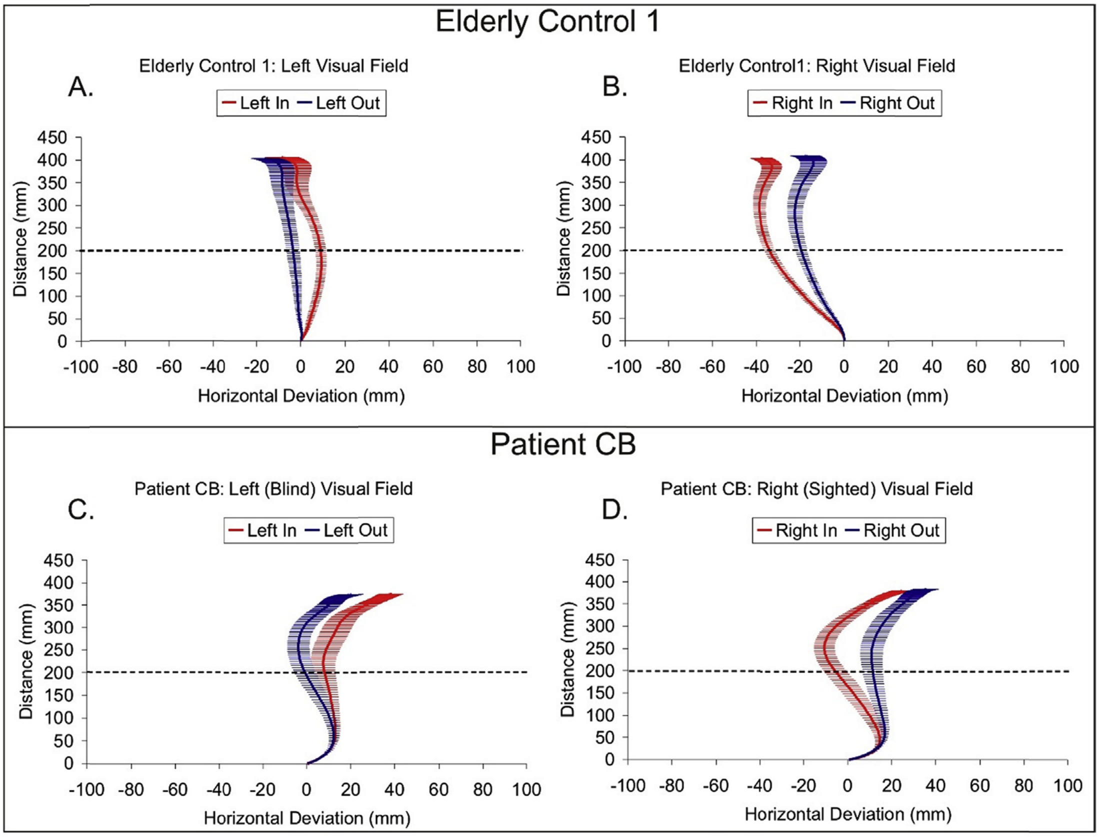

Fig. 1 – Real-time obstacle avoidance in the left and right visual fields for a healthy older control (top panel) and patient C.B. (bottom panel). Red lines indicate the average reach trajectory (±SE) when the obstacle was placed in the "in" position where it was more of an obstacle to the reaching hand. Blue lines indicate the average reach trajectory (±SE) when the obstacle was placed in the "out" position where it was less of an obstacle to the reaching hand. The black dotted line represents the depth at which the obstacles were placed in the workspace. Note that for both the elderly control, and patient CB, reach trajectories deviate away from the obstacle more when it is placed in the "in" position when it is closer to the reaching hand, compared to the "out" position, where the obstacle is further away from the reaching hand. Most notably, panel C clearly demonstrates that patient CB remains sensitive to the position of the obstacles in his blind (left) field. However, note how the reach trajectories in the blind field only show statistically significant separation beyond 20 cm into the reach (i.e., the rear edge of the obstacle) indicating that obstacle avoidance is not entirely "normal" in the patient's blind field. Reprinted with permission from (Striemer, Chapman, et al., 2009).

perceived impact of what essentially amount to null findings. One of the most important statements they make in this regard is:

> "According to the perception-action model (Milner & Goodale, 2006, 2008) it is assumed that both the dorsal and ventral stream obtain their visual input primarily from area V1. However, more recently, it has been argued that obstacle avoidance behaviour can actually proceed normally without input from V1 (Striemer, Chapman, et al., 2009) implying that some functions in the dorsal stream primarily rely on visual information mediated via subcortical pathways (Ross et al., 2018, p. 4)."

There are several important points to make in response to these misguided statements. 1) At no point in our 2009 paper (or any other paper) did we ever say that V1 input was not important for dorsal stream function. 2) At no point in our 2009 paper did we ever say that obstacle avoidance was "normal" in our patient's blind field. In fact, there are data in the paper itself that clearly indicate that C.B.'s obstacle avoidance was not completely normal. Specifically, C.B.'s reach trajectories showed significant sensitivity to changes in obstacle position only at 25 cm into the reach (Fig. 1C) which corresponds to the rear edge of the obstacle (a point we will return to later). We suggested that this might have been due to disruptions in depth perception following damage to V1. Despite this, C.B. still showed a clear (and statistically significant) separation between his reach trajectories based on the changing location of the obstacles in his blind field (Fig. 1C). 3) Finally, nowhere in our 2009 paper did we say that obstacle avoidance relies primarily on input via subcortical pathways. The fact that C.B. was sensitive to the position of obstacles in his blind field merely indicates that it is possible for obstacle avoidance to occur without V1 input, not that V1 input makes no contribution to obstacle avoidance. In summary, we find it concerning that the primary motivation for Ross et al.'s (2018) study was to essentially challenge claims that were never made in our original paper. In the next section we will examine several methodological shortcomings that limit the interpretability of Ross et al.'s (2018) findings, and virtually guaranteed that they would find a null-effect.

2. When a group study is really a single case study: or, when 5 + 1 = 1

One of the critical pieces of evidence that Ross et al. (2018) use to argue that obstacle avoidance can occur only with input from occipital cortex is the fact that they failed to observe any evidence of obstacle avoidance in six patients with visual field defects following damage to occipital cortex. At first glance this seems like a decisive failure to replicate our 2009 findings. If so, this would cast serious doubt on our earlier work, and instead suggest (as Ross et al., 2018 do) that it is not possible to avoid obstacles without V1 input. If one digs a bit deeper, however, it becomes obvious that Ross et al.'s data are, in fact, a single case study with five additional patients who are not comparable to patient C.B. (the patient from our 2009 paper).

To put things in a clearer context, let's start by discussing C.B., the patient from our earlier 2009 paper. As we reported in our 2009 paper, patient C.B. suffered a right posterior cerebral artery stroke at age 75. This resulted in a dense left visual field hemianopia that was verified via Goldman perimetry at the time of testing. Before we ran the obstacle avoidance experiment with patient C.B. we screened him for evidence of blindsight-the ability to detect, localize, and/or discriminate visual stimuli in the absence of visual awareness (Cowey, 2010; Danckert & Rossetti, 2005; Weiskrantz, 1986; Weiskrantz, Warrington, Sanders, & Marshall, 1974). To screen C.B. for evidence of blindsight, we used redundant target and target pointing localization tasks which have been employed in numerous previous studies (e.g., Corbetta, Marzi, Tassinari, & Aglioti, 1990; Leh, Mullen, & Ptito, 2006; Marzi, Mancini, Metitieri, & Savazzi, 2009; Marzi, Tassinari, Aglioti, & Lutzemberger, 1986; Weiskrantz, 1986; Weiskrantz et al., 1974). As reported in our 2009 paper C.B. demonstrated a significant redundant target effect such that he was faster to respond when targets appeared in his sighted and blind fields simultaneously, compared to when only a single target appeared in his sighted field. However, C.B. was not able to localize the position of targets in his blind field by pointing. In summary, C.B. demonstrated clear evidence of blindsight for one task (i.e., the redundant target effect) but no evidence of blindsight with the other task (i.e., target localization). It is important to point out that these data are not out of the ordinary, as there are many blindsight patients who show residual abilities for some tasks, but not others (e.g., Corbetta et al., 1990; Whitwell, Striemer, Nicolle, & Goodale, 2011). While it is not entirely clear why this occurs, it may have to do with differences in the spared visual pathways amongst different patients (Danckert & Rossetti, 2005).

Now let us examine the patients tested by Ross et al. (2018). They presented data from six patients (four with left hemisphere lesions, two with right hemisphere lesions) with visual field defects resulting from damage to occipital cortex, as well as other surroundings structures. Ross et al. also tested each of their patients for evidence of blindsight using the same two tasks that we used in our 2009 paper (i.e., the redundant target and target localization tasks). Based on their performance in these tasks only one patient (Patient 4) in their sample of six patients demonstrated any objective evidence of blindsight. Thus, only one patient in their entire sample can be considered as comparable to patient C.B. from our 2009 paper, as one would never expect to see any evidence of obstacle avoidance in the blind field of a patient who did not demonstrate blindsight in some other test involving processing visual stimuli unconsciously in the blind field. Now that we see their sample for what it is, a single case study, let us examine that patient in more detail.

Patient 4 appears, on the surface, to be directly comparable to our patient C.B. She demonstrated evidence of blindsight on both the redundant target and target localization tasks. So, the important question that remains is this: Why then did she still fail to demonstrate any evidence of obstacle avoidance in her blind field? Although this patient appears to be similar to C.B., she does differ from C.B. in one critical way. Specifically, her lesion is much more extensive than C.B.'s, and extends from visual cortex into the occipital–parietal cortex and the underlying white matter in the left hemisphere (Fig. 2). This clearly places Patient 4's lesion in the dorsal visual stream (Karnath & Perenin, 2005; Milner & Goodale, 2006; Perenin & Vighetto, 1988).

The importance of this observation cannot be understated as we argued in our 2009 paper that the dorsal stream was responsible for C.B.'s preserved sensitivity to the presence of obstacles in his blind field. This is based on the fact that C.B.'s dorsal stream was undamaged (Fig. 3), and that previous studies in patients with damage to the dorsal stream failed to show evidence of obstacle avoidance in the contralesional field when reaching in real-time (Rice et al., 2008; Schindler et al., 2004). In addition, there is neuroimaging evidence for the engagement of posterior parietal cortex during obstacle avoidance healthy adults (Chapman, Gallivan, Culham, & Goodale, 2011). Therefore, if a patient has damage to his or her dorsal stream (as well as occipital cortex), then it is likely that they would not show any obstacle avoidance behaviour in their blind field. Note that Patient 4 also dramatically undershot the position of the targets presented in her blind field in the pointing localization task. This pattern of pointing performance is consistent with what is typically observed in patients with optic ataxia following dorsal stream damage. That is, reaching errors tend to increase with target eccentricity in the ataxic field (Pisella et al., 2007, 2009; Rossetti, Pisella, & Vighetto, 2003; Striemer, Locklin, et al., 2009). To emphasize this point, we re-plotted the data for the target localization task for Patient 4 from Ross et al.'s study. Specifically, we calculated pointing errors by using the horizontal pointing distance for Patient 4 reported in their original graph, the reported target positions (in degrees of visual angle), and a viewing distance of 500 mm (as reported in Ross et al.). When these data are plotted as pointing errors (as opposed to pointing distance), it quite clear that accuracy becomes much worse with increasing target eccentricity in the contralesional (i.e., blind) field, just as one would expect in a patient with optic ataxia (Fig. 4). Thus, given Patient's 4's dorsal-stream

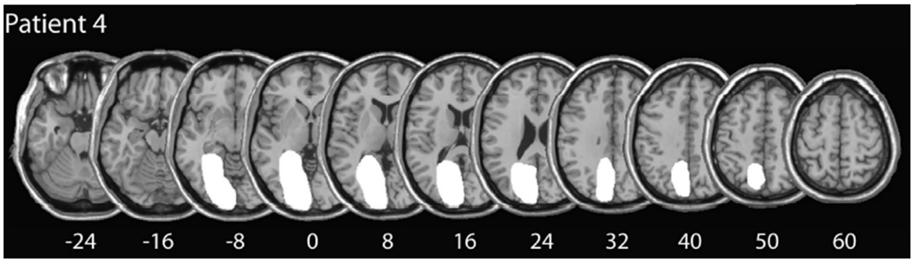

Fig. 2 – Patient 4's lesion map taken from Figure 1 in Ross et al. (2018). Note the clear extension of the patient's lesion into the superior parietal–occipital cortex (i.e., the dorsal stream) in the left hemisphere.

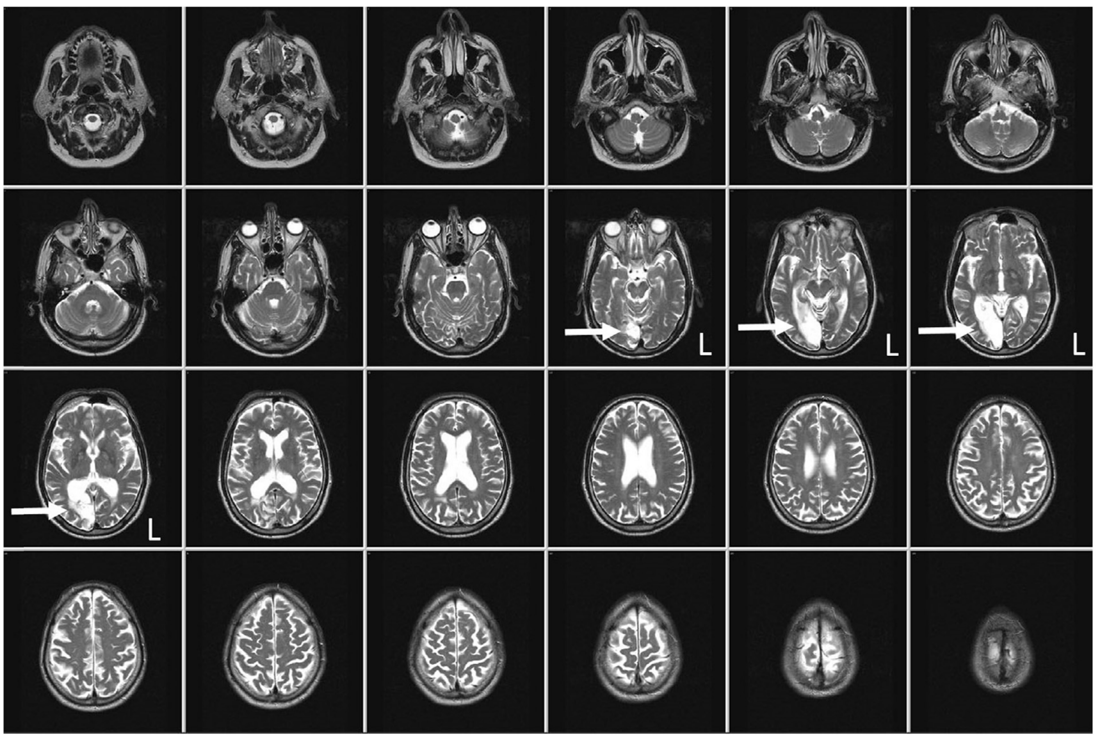

Fig. 3 – A T2 MRI scan of patient C.B.'s right occipital injury that extends into the optic radiations. Note the absence of any damage to structures in the left or right posterior parietal cortex. Anatomical images are presented in radiological convention with left and right reversed.

lesion, and optic ataxia-like pointing behaviour, one would never expect to observe obstacle avoidance in her contralesional (blind) field. Therefore, while having an intact dorsal stream does not guarantee that a blindsight patient would be able to localize a target accurately in their blind field, an intact dorsal stream does appear to be a necessary prerequisite to observe obstacle avoidance.

In the next section we take a closer look at some of the other methodological limitations of Ross et al. (2018) that also made it more likely that they would fail to replicate our earlier our earlier 2009 findings.

3. Other methodological considerations

In the previous section we detailed how the patient sample studied by Ross et al. (2018) virtually ensured that they would find a null-effect. First, only one of the six patients tested demonstrated any evidence of blindsight (i.e., Patient 4). And second, this patient's lesion extended into the dorsal visual pathway, severely reducing the chance of showing avoidance behaviour in their contralesional (i.e., blind) field (Rice et al., 2008; Schindler et al., 2004). In addition to these limitations, we will argue that the setup of the obstacle avoidance task employed by Ross et al. (2018), as well as their analysis strategy, further ensured that they would find a null-effect.

First, let us examine the obstacle avoidance task employed by Ross et al. (2018). Given that one of the primary purposes of their study was to “replicate” our earlier 2009 findings, one would assume that their methods would closely match the methods that we employed in order to facilitate a direct comparison of the two studies. In their study, however, Ross et al. placed obstacles either 6 cm or 10 cm away from midline in either the left or right visual field. In our 2009 study, our

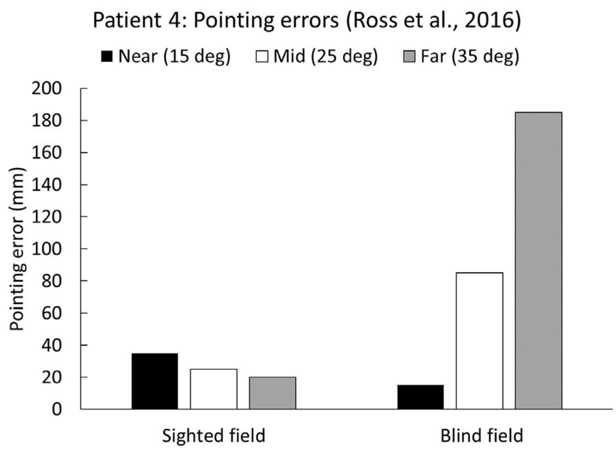

Fig. 4 — Target localization data from Patient 4 (see Figure 3 in Ross et al., 2018) replotted as pointing errors using the reported horizontal pointing distance (in mm), the reported target eccentricities (15°, 25°, and 35°), and a viewing distance of 500 mm. Note the large increase in pointing errors with increasing target eccentricity in the blind field. This pattern of reach errors is consistent with those seen in patients with optic ataxia following dorsal stream damage (e.g., Rossetti et al., 2003; Striemer, Locklin, et al., 2009).

closest obstacle (i.e., the "in" position) was 10 cm from the reaching hand and our furthest obstacle (i.e., the "out" position) was 15 cm from the reaching hand. Note that healthy older and younger controls demonstrated clear obstacle avoidance when obstacles were placed in these positions (see Fig. 1C, as well as the Supplementary Information in our 2009 paper). In addition, C.B. demonstrated clear evidence of obstacle avoidance when obstacles were placed in these positions in both his sighted as well as his blind field (Fig. 1C). The reason this difference in the arrangement of the obstacles could be important is that, if the obstacles are placed even closer to the reaching hand (4–5 cm closer in the Ross et al. study), then this makes it much more likely that a participant will collide with and knock over an obstacle during a trial. This is especially important in a patient's blind field. Specifically, if a patient believes that there are no obstacles present in the blind field (i.e., the patient reports "seeing nothing"), and he or she collides with an unseen obstacle during the reach, this could immediately change how the patient behaves on subsequent trials. That is, on subsequent trials when the patient "sees nothing" in the blind field, he or she may assume that there is always an obstacle present, and adopt a cautious reach strategy that is unlikely to reveal any sensitivity to obstacles in the blind field. Thus, part of the reason we placed objects further away from the reaching hand was to minimize the chances of such collisions occurring. This is also why we felt it was important to note in our 2009 paper that C.B. never collided with any objects in his blind field. Unfortunately, data on obstacle collisions in the blind field were not reported by Ross et al. (2018).

Another major difference between our obstacle avoidance task and the obstacle avoidance task utilized by Ross et al. (2018) is the size of the obstacles used. Specifically, we used obstacles that were 4 cm × 4 cm × 25 cm rectangular objects. In contrast, the obstacles used by Ross et al. were only 1 cm × 1 cm × 15 cm. Thus, the 2D surface area of the obstacles used in our study was 100 cm^2 (4 cm × 25 cm), whereas the 2D surface area of the obstacles used by Ross et al. was only 15 cm^2 (1 cm × 15 cm). Although the difference in size of the obstacles used between the two studies was acknowledged by Ross et al., they dismissed it as unimportant because their smaller obstacles were capable of eliciting avoidance behaviour in each patient's sighted field. However, although a smaller obstacle might be sufficient to elicit obstacle avoidance in a normally sighted field, it may be insufficient to elicit obstacle avoidance in a blind field. Specifically, it is well known that stimulus size plays an important role in the detection of stimuli in blindsight, such that patients with blindsight are more likely to show residual visual processing for larger stimuli (for a review see Sahraie, 2007). Thus, by using smaller obstacles, Ross et al. made it harder to observe obstacle avoidance effects in a blind field.

A final methodological difference between the obstacle avoidance task we used, and that employed by Ross et al., is that their obstacles differed significantly in their stability. While the obstacles that we used in our 2009 paper were free standing, and easy to knock over (as mentioned only a 4 cm × 4 cm base for a 25 cm tall object), the obstacles used by Ross et al., were LEGO towers which we assume were fixed to the LEGO baseplate that they used to present stimuli on the table. Since recent work shows that the identity of an object (e.g., whether a to-be-avoided water glass is full or empty) influences obstacle avoidance behaviour (de Haan, Van der Stigchel, Nijnens, & Dijkerman, 2014), it is entirely possible that this factor also contributed to the lack of avoidance observed in the patient's blind field. Specifically, avoidance behaviour is reduced when the perceived consequence of collision is lower (e.g., when the glass is empty). We argue that a LEGO tower firmly secured to a LEGO baseplate would have a lower perceived consequence of collision, leading to reduced avoidance. Importantly, since this difference in obstacle stability was embedded as part of their experimental design, any perception of the consequence of a collision would extend to all trials (e.g., in a blind or sighted field), since participants would correctly assume that all objects would be placed securely on the LEGO baseplate.

Another important difference between our study and that of Ross et al. (2018) was the data analysis strategy that they used. Specifically, in our 2009 paper, we presented a detailed analysis of trials in which a single obstacle was placed in either the sighted or the blind field to argue that patient C.B. was sensitive to the position of obstacles in his blind field (see the Supplementary Material in our 2009 paper for data from two obstacle trials).

Ross et al. suggest, however, that the two obstacle trials, where obstacles are presented in the left and right visual fields simultaneously, are a better test of their hypothesis. Specifically, they state:

> "Furthermore, we think that the two-obstacle paradigm is the more appropriate task as it may provide a more sensitive indicator of a patient's ability to use visual information from their blind field for movement planning and control than the single obstacle task. In the single obstacle

> version the entire space opposite the obstacle is free of obstacles and therefore there is no reason for why participants should not simply direct their hand to this empty space thereby keeping a large distance from any obstacle placed in one half of the workspace. However, the further the hand is moved away from an obstacle the less likely it becomes that obstacle position will still affect movement path selection. In contrast, when two obstacles are placed into the two halves of the workspace the optimal strategy would be to find a movement path that passes midway between the two obstacles, thereby minimising the risk of collision with any of them. Importantly, this strategy requires participants to take the position of both obstacles into account. Hence, we think that a two-obstacle paradigm may provide a more sensitive task to detect a patient's ability to use visual information from their blind field for obstacle avoidance (Ross et al., 2018, p. 6–7)."

The important point to make in regard to this statement is that, for a normally sighted individual, the two obstacle condition will allow one to examine how each obstacle influences avoidance behaviour. However, for a person who is blind in one visual field (like our patient C.B.), it is naïve to assume that an obstacle in the sighted field will be weighted equally when planning a reach when compared to an obstacle that is presented in a blind field that the patient is entirely unaware of. The assumption that obstacles in the blind field would be treated the same as obstacles in the sighted field is based on the faulty assumption put forward by Ross et al. that obstacle avoidance in a blind field should "proceed normally" following damage to V1, a point we addressed earlier. When understood from this context, it is quite clear why single obstacle trials are a more appropriate measure of obstacle avoidance for a patient with a blind field. Furthermore, if a patient were simply hedging their bets that an obstacle had been placed in the blind field by reaching into good field whenever no obstacle was detected in the workspace (as suggested in the quote above from Ross et al.) then they would not show any sensitivity to the position of the obstacle in the blind field. C.B., however, was sensitive to the changing position of the obstacle in the blind field, clearly indicating that some sort of obstacle avoidance mechanism was still at work.

Another major difference in the data analysis strategy used by Ross et al. (2018) is that they only ever analysed the position of the fingertip at the exact point that it passed by the obstacle. This analysis strategy also seems to be based on the naïve assumption that obstacle avoidance should be "normal" in a blind field in a patient with a V1 lesion. In our 2009 paper, we presented the average reach trajectory for each obstacle condition for our patient, as well as our elderly and young controls (see the Supplementary Information in our 2009 paper). In addition, we also presented the difference in the position of the index finger for "out" minus "in" conditions at 5 cm increments from the start to the end of the reach (see Supplementary Figures S5–S7 in our 2009 paper). This method is much more likely to capture significant differences between conditions because it does not implicitly assume that only one position during the reach trajectory is relevant to observe obstacle avoidance while essentially ignoring data from all other positions. Importantly, this analysis demonstrated that our patient's (C.B.) reach trajectories were sensitive to the changing position of the obstacles in his blind field at 25 cm into the reach, that is, 5 cm past the front edge of the obstacle. Note that the separation between reach trajectories for obstacles in the "in" *vs* "out" positions in C.B.'s blind field started well before the front edge of the obstacle, but differed significantly only at 25 cm into the reach (Fig. 1C). Thus, if we had used the same analysis strategy as Ross et al., we would have missed the significant difference in our own patient entirely.

Finally, Ross et al.'s bold assertion that our results in patient C.B. may "simply reflect a chance finding (p. 23)" because they were based on "one session for only one patient" where "a few outliers can generate a significant effect (p. 23)" is baseless claim. Our data clearly demonstrate a statistically significant obstacle avoidance effect in C.B.'s blind field. This effect could not have been due to "outliers" as all outliers were removed prior to conducting the statistical analyses. Furthermore, we collected data from 16 trials for each obstacle avoidance condition in patient C.B. (as noted in our 2009 paper) which is more trials per condition than was collected (i.e., 12 trials per condition) for any of the patients tested by Ross et al. So, in summary, while Ross et al., would like to try and convince readers that a clear and statistically significant effect from a single case study in our 2009 paper is not enough evidence to suggest that obstacle avoidance is possible without V1 input; they are more than happy to argue that a null-effect in one patient with a dorsal stream lesion (in a study with a host of additional methodological limitations) is more than enough evidence to dismiss our findings.

4. Conclusion

To summarize, Ross et al.'s "failure to replicate" our 2009 findings is based on data from a patient population where one would not even expect to observe obstacle avoidance in a blind field. Specifically, only one out of the six patients tested showed any objective evidence of blindsight, so one would never expect to see any evidence of obstacle avoidance in the blind fields of these patients. Furthermore, the single blindsight patient in their sample also had a dorsal-stream lesion in the same hemisphere which previous studies have demonstrated would prevent any obstacle avoidance effects on the contralesional side (i.e., in the patient's blind field) (Rice et al., 2008; Schindler et al., 2004). Given that Ross et al. have no valid data with which to claim a failure to replicate, any conclusions they reach regarding our earlier study that are based on these same data are, by extension, invalid.

In addition to having a non-comparable patient sample, the obstacle avoidance task employed by Ross et al. (2018) also suffered from a number of limitations that made it more likely that they would find a null effect. Specifically, they used an obstacle avoidance task with obstacles that were likely too small to elicit avoidance behaviour in a blind field, were placed at locations quite different those in our study, and were significantly more stable since they were physically attached to the table. Furthermore, Ross et al. also employed an unnecessarily restrictive analysis strategy that focused only on a single point in the reach trajectory. When these significant methodological limitations are combined with their non-comparable patient sample, it is not surprising that no significant obstacle avoidance effects were observed in any of their patient's blind fields.

So, in the end, what, if anything, have we learnt from Ross et al.'s (2018) study? In our opinion, all we can really conclude from Ross et al.'s data are 1) that patients without blindsight do not demonstrate obstacle avoidance in their blind field, and 2) a patient with blindsight with a dorsal stream lesion did not demonstrate obstacle avoidance in their blind field. When seen in this light Ross et al.'s data could actually be interpreted as providing partial support for the hypothesis we put forward in our 2009 paper. Namely, that the dorsal stream was responsible for the obstacle avoidance effect we observed in our blindsight patient C.B. Of course, one needs to be careful when making statements such as these because, as has become clear by now, one should not make bold theoretical claims based exclusively on null effects.

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REFERENCES

Chapman, C. S., Gallivan, J. P., Culham, J. C., & Goodale, M. A. (2011). Mental blocks: fMRI reveals top-down modulation of early visual cortex when obstacles interfere with grasp planning. *Neuropsychologia, 49*(7), 1703–1717. http://dx.doi.org/10.1016/j.neuropsychologia.2011.02.048.

Corbetta, M., Marzi, C. A., Tassinari, G., & Aglioti, S. (1990). Effectiveness of different task paradigms in revealing blindsight. *Brain: a Journal of Neurology, 113*(Pt 3), 603–616.

Cowey, A. (2010). The blindsight saga. *Experimental Brain Research,* 200(1), 3–24. http://dx.doi.org/10.1007/s00221-009-1914-2.

Danckert, J., & Rossetti, Y. (2005). Blindsight in action: What can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience and Biobehavioral Reviews, 29*(7), 1035–1046.

de Haan, A. M., Van der Stigchel, S., Nijnens, C. M., & Dijkerman, H. C. (2014). The influence of object identity on obstacle avoidance reaching behaviour. *Acta Psychologica, 150*, 94–99. http://dx.doi.org/10.1016/j.actpsy.2014.04.007.

Karnath, H. O., & Perenin, M. T. (2005). Cortical control of visually guided reaching: Evidence from patients with optic ataxia. *Cerebral Cortex, 15*(10), 1561–1569.

Leh, S. E., Mullen, K. T., & Ptito, A. (2006). Absence of S-cone input in human blindsight following hemispherectomy. *European Journal of Neuroscience, 24*(10), 2954–2960. http://dx.doi.org/10.1111/j.1460-9568.2006.05178.x. EJN5178 [pii].

Marzi, C. A., Mancini, F., Metitieri, T., & Savazzi, S. (2009). Blindsight following visual cortex deafferentation disappears with purple and red stimuli: A case study. *Neuropsychologia, 47*(5), 1382–1385. http://dx.doi.org/10.1016/j.neuropsychologia.2009.01.023. S0028-3932(09)00026-8 [pii].

Marzi, C. A., Tassinari, G., Aglioti, S., & Lutzemberger, L. (1986). Spatial summation across the vertical meridian in hemianopics: A test of blindsight. *Neuropsychologia, 24*(6), 749–758.

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). New York: Oxford University Press.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia, 46*(3), 774–785. S0028-3932(07)00354-5 [pii], http://dx.doi.org/10.1016/j.neuropsychologia.2007.10.005.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain: a Journal of Neurology, 111*(Pt 3), 643–674.

Pisella, L., Sergio, L., Blangero, A., Torchin, H., Vighetto, A., & Rossetti, Y. (2009). Optic ataxia and the function of the dorsal stream: Contributions to perception and action. *Neuropsychologia, 47*(14), 3033–3044. http://dx.doi.org/10.1016/j.neuropsychologia.2009.06.020. S0028-3932(09)00273-5 [pii].

Pisella, L., Striemer, C., Blangero, A., Gaveau, V., Revol, P., Salemme, R., … Rossetti, Y. (2007). Perceptual deficits in optic ataxia? In P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition: Attention and performance XXII* (pp. 47–72). Oxford: Oxford University Press.

Rice, N. J., Edwards, M. G., Schindler, I., Punt, T. D., McIntosh, R. D., Humphreys, G. W., … Milner, A. D. (2008). Delay abolishes the obstacle avoidance deficit in unilateral optic ataxia. *Neuropsychologia, 46*(5), 1549–1557. http://dx.doi.org/10.1016/j.neuropsychologia.2008.01.012. S0028-3932(08)00018-3 [pii].

Rossetti, Y., Pisella, L., & Vighetto, A. (2003). Optic ataxia revisited: Visually guided action versus immediate visuomotor control. *Experimental Brain Research, 153*(2), 171–179.

Ross, A. I., Schenk, T., Billino, J., Macleod, M. J., & Hesse, C. (2018). Avoiding unseen obstacles: Subcortical vision is not sufficient to maintain normal obstacle avoidance behaviour during reaching. *Cortex, 98*, 177–193.

Sahraie, A. (2007). Induced visual sensitivity changes in chronic hemianopia. *Current Opinion in Neurology, 20*(6), 661–666. http://dx.doi.org/10.1097/WCO.0b013e3282f1c70f00019052-200712000-00011.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: Evidence from optic ataxia. *Nature Neuroscience, 7*(7), 779–784.

Striemer, C. L., Chapman, C. S., & Goodale, M. A. (2009). "Real-time" obstacle avoidance in the absence of primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 106*(37), 15996–16001. http://dx.doi.org/10.1073/pnas.0905549106.

Striemer, C. L., Locklin, J., Blangero, A., Rossetti, Y., Pisella, L., & Danckert, J. (2009). Attention for action? Examining the link between attention and visuomotor control deficits in a patient with optic ataxia. *Neuropsychologia, 47*(6), 1491–1499. http://dx.doi.org/10.1016/j.neuropsychologia.2008.12.021. S0028-3932(08)00501-0 [pii].

Weiskrantz, L. (1986). *Blindsight: A case study and implications.* Toronto: Oxford University Press.

Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain: a Journal of Neurology, 97*(4), 709–728.

Whitwell, R. L., Striemer, C. L., Nicolle, D. A., & Goodale, M. A. (2011). Grasping the non-conscious: Preserved grip scaling to unseen objects for immediate but not delayed grasping following a unilateral lesion to primary visual cortex. *Vision Research, 51*(8), 908–924. http://dx.doi.org/10.1016/j.visres.2011.02.005. S0042-6989(11)00045-9 [pii].

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