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Abstract:

Previous research suggests that the implicit recognition of emotional expressions may be carried out by pathways that bypass primary visual cortex (V1) and project to the amygdala. Some of the strongest evidence supporting this claim comes from case studies of "affective blindsight" in which patients with V1 damage can correctly guess whether an unseen face was depicting a fearful or happy expression. In the current study, we report a new case of affective blindsight in patient MC who is cortically blind following extensive bilateral lesions to V1, as well as face and object processing regions in her ventral visual stream. Despite her large lesions, MC has preserved motion perception which is related to sparing of the motion sensitive region MT+ in both hemispheres.

To examine affective blindsight in MC we asked her to perform gender and emotion discrimination tasks in which she had to guess, using a two-alternative forced-choice procedure, whether the face presented was male or female, happy or fearful, or happy or angry. In addition, we also tested MC in a four-alternative forced-choice target localization task. Results indicated that MC was not able to determine the gender of the faces (53% accuracy), or localize targets in a forced-choice task. However, she was able to determine, at above chance levels, whether the face presented was depicting a happy or fearful (67%, p=.006), or a happy or angry (64%, p=.025) expression. Interestingly, although MC was better than chance at discriminating between emotions in faces when asked to make rapid judgments, her performance fell to chance when she was asked to provide subjective confidence ratings about her performance. These data lend further support to the idea that there is a non-conscious visual pathway that bypasses V1 which is capable of processing affective signals from facial expressions without input from higher-order face and object processing regions in the ventral visual stream.

1. Introduction:

In 1974 Weiskrantz and colleagues (Weiskrantz, Warrington, Sanders, & Marshall, 1974) published a landmark study in which they demonstrated that a patient, now known as DB, was able to accurately respond to stimuli in a blind portion of his left visual field following a neurosurgery that was conducted to remove his right occipital pole. Specifically, when targets were presented in varying locations in his blind (left) visual field, DB could accurately "guess" the target's position by moving his eyes (see also Poppel, Held, & Frost, 1973) or his hand to the location despite his inability to "see" the targets. Using two-alternative forced choice procedures, DB was shown to discriminate stimuli on the basis of their orientation (i.e., horizontal vs. vertical), form (i.e., X vs. O), and color (red vs. green) despite his insistence that he "saw nothing" and was "completely guessing." In an attempt to describe their findings Weiskrantz et al. (1974) coined the term "blindsight" as an oxymoron to refer to the paradoxical ability to "see" in the absence of a conscious visual experience (see also Weiskrantz, 1986). Furthermore, Weiskrantz and colleagues suggested that blindsight might be explained by intact visual projections from the retina to other posterior visual association areas via connections with the superior colliculus (see also Lyon, Nassi, & Callaway, 2010).

The importance of these seminal findings cannot be understated as they had a tremendous influence on the subsequent study of the relationship between different visual pathways and non-conscious behaviour in humans and animals (for reviews see Cowey, 2010; Danckert & Rossetti, 2005), as well as the philosophical study of consciousness (for example, Block, 1995; Brogaard, 2011). Furthermore, the discovery of blindsight proved to be an important precursor to the later development of the highly influential "two visual systems" hypothesis (Goodale & Milner, 1992; Milner & Goodale, 2006, 2008). In fact, since Weiskrantz and colleagues' (1974) original study

numerous subsequent investigations have demonstrated a variety of different residual perceptual abilities in individuals with blindsight such as color (e.g., Danckert, Maruff, Kinsella, de Graaff, & Currie, 1998; Stoerig & Cowey, 1992; Stoerig, Kleinschmidt, & Frahm, 1998) and form processing (e.g., Danckert et al., 1998), spatial attention (Kentridge, Heywood, & Weiskrantz, 2004), speeded processing of redundant visual signals (e.g., Corbetta, Marzi, Tassinari, & Aglioti, 1990; Leh, Mullen, & Ptito, 2006; Marzi, Tassinari, Aglioti, & Lutzemberger, 1986; Striemer, Chapman, & Goodale, 2009), and motion discrimination (e.g., Barbur, Watson, Frackowiak, & Zeki, 1993; Zeki & Ffytche, 1998). In addition, numerous studies have also demonstrated a variety of spared visuomotor abilities in the blind field such as target localization (e.g., Corbetta et al., 1990; Whitwell, Striemer, Nicolle, & Goodale, 2011), obstacle avoidance (de Gelder et al., 2008; Striemer et al., 2009; Striemer, Chapman, & Goodale, 2017), and the ability to scale one's grip to objects (Perenin & Rossetti, 1996; Whitwell et al., 2011).

Another landmark paper in 1999 (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999) reported the first demonstration of what is now known as "affective blindsight" in the well-studied blindsight patient GY (for reviews see Celeghin, de Gelder, & Tamietto, 2015; Tamietto & de Gelder, 2010). Using forced choice procedures, they demonstrated that GY could reliably discriminate between happy vs. fearful, angry vs. sad, or angry vs. fearful facial expressions. In addition, GY's performance improved when he was presented with brief movie clips of moving faces depicting different emotions, compared to still frame pictures. Based on these findings, de Gelder et al. (1999) hypothesized that GY's affective blindsight was linked to a visual pathway to extrastriate areas and the amygdala via the superior colliculus and/or pulvinar, bypassing V1 altogether. This hypothesis was supported by a number of additional findings. Specifically, subsequent functional neuroimaging studies demonstrated increased activity in the amygdala in

patient GY when fearful faces were presented to his blind field (de Gelder, Morris, & Dolan, 2005; Morris, DeGelder, Weiskrantz, & Dolan, 2001). In fact, this pattern of activity closely resembled the activity observed in the amygdala in healthy participants when they are presented with "unseen" (i.e., masked) fearful faces (e.g. Morris, Ohman, & Dolan, 1999; Whalen et al., 1998). Furthermore, the connections between the superior colliculus and the amygdala, as well as the pulvinar and the amygdala, can be shown in healthy adults using diffusion tensor imaging (DTI) (Tamietto, Pullens, de Gelder, Weiskrantz, & Goebel, 2012). Importantly, these same connections are observed in both hemispheres in affective blindsight patient GY. Although GY's damaged (left) hemisphere shows fewer connections amongst the amygdala, colliculus, and pulvinar relative to healthy controls, GY shows more colossal connections linking the posterior hemispheres (Tamietto et al., 2012). Finally, another recent study by Rafal and colleagues (Rafal et al., 2015) used DTI to demonstrate connections between the superior colliculus and amygdala in both human and non-human primates.

The notion that affective signals can be processed in the absence of visual awareness was further supported in recent work by Bertini, Cecere, Ladavas, and others examining groups of patients with visual field defects (Bertini, Cecere, & Ladavas, 2013, 2017; Cecere, Bertini, Maier, & Ladavas, 2014). Specifically, these studies have demonstrated that "fearful" faces presented in the blind field facilitated responses to stimuli (i.e., "happy" faces, or gabor patches) that were simultaneously presented in the sighted field (Bertini et al., 2013, 2017; Cecere et al., 2014). This non-conscious enhancement occurred even when the emotional information was not relevant to the task (Bertini et al., 2013). It is important to note that none of the patients in any of these studies was above chance at discriminating between different facial emotions when the faces were presented exclusively within the blind field. Furthermore, none of the patients studied

demonstrated any other symptoms of blindsight (Bertini et al., 2013, 2017; Cecere et al., 2014). In short, these studies do not address the question of whether or not affective stimuli restricted to the blind field can drive reliable discriminative performance. Thus, an additional positive test of this question would constitute an important finding.

Although the initial demonstrations of affective blindsight in patient GY were ground-breaking, one important but unanswered question concerned the degree to which GY's intact (left) visual field might play a role in his ability to discriminate emotional content from faces. This important question was addressed in a study by Pegna and colleagues (Pegna, Khateb, Lazeyras, & Seghier, 2005) who studied patient TN. TN was left completely cortically blind following two successive strokes that resulted in extensive bilateral damage to occipital-temporal cortex, including bilateral damage to V1. Following his strokes, TN was unable to discriminate between a square and a circle, or between male and female faces using two-alternative forced choice procedures. Despite these deficits, TN was able to discriminate between happy vs. sad and happy vs. fearful faces. Furthermore, a subsequent functional neuroimaging experiment in the same paper demonstrated that there was significant activity in TN's right amygdala when he was presented with pictures of emotional faces, with fearful faces inducing the largest response. Thus, Pegna et al. (2005) concluded that affective blindsight can occur in the complete absence of conscious vision, and requires input from the amygdala.

Since Pegna's original (2005) report, patient TN has been studied extensively. While subsequent experiments with patient TN demonstrate that he can avoid obstacles while walking (de Gelder et al., 2008) and that he processes some visual stimuli more effectively than others (i.e., bodies, direction of eye gaze; Burra et al., 2013; Van den Stock et al., 2014), TN's ability to discriminate between different emotions using behavioural measures has not been able to be

replicated. Specifically, although subsequent neuroimaging studies with TN using EEG and fMRI have clearly indicated that neural responses in the amygdala, as well as temporal regions, are modulated by the emotional valence of faces (Andino, Menendez, Khateb, Landis, & Pegna, 2009; Burra et al., 2013), these subsequent studies have not been able to replicate TN's ability to *discriminate behaviourally* between the different emotions depicted by these faces (Andino et al., 2009; de Gelder et al., 2008).

In the current study, we present an important replication of Pegna et al.'s (2005) behavioural findings in patient MC who was left completely blind to static (i.e., non-moving) stimuli following two successive strokes that resulted in extensive bilateral damage to occipital and ventral temporal cortex, and the right posterior parietal cortex (Dutton, 2003). In addition to replicating Pegna et al.'s (2005) important results in patient MC, the current study also demonstrates that 1) MC's ability to discriminate the emotional content of faces exists in the absence of any ability to determine the gender of the face, or to localize targets by forced choice; 2) MC's affective blindsight performance deteriorates when she is asked to introspect and provide subjective confidence ratings about her performance; and 3) input from object and face processing regions in the ventral visual stream are not required in order for affective blindsight to be observed.

2. Methods:

2.1 Participants.

2.1.1 Patient MC

In the current study we examined gender and affective discrimination, as well as target localization, in patient MC. Additional details regarding MC's case history, as well as her

remarkable spared abilities are reported elsewhere (Arnott, Cant, Dutton, & Goodale, 2008; Culham, Witt, Valyear, Dutton, & Goodale, 2008; Dutton, 2003; Snow, Goodale, & Culham, 2015; Thaler et al., 2016; Wolf et al., 2008; Wood, Chouinard, Major, & Goodale, 2016). Briefly, MC is a right-handed female who was born in 1969 and worked as a secretary prior to her injury. MC was 42 years old at the time of testing. At age 30, MC contracted a respiratory infection which led to a severe stroke resulting in extensive bilateral lesions to her occipital lobes, as well as her ventral temporal cortices, and right posterior parietal cortex (Figure 1a).

Following her extensive lesions MC was left completely blind when tested using static perimetry (see Dutton, 2003; Thaler et al., 2016). However, MC is able to detect moving targets (see Dutton, 2003; Thaler et al., 2016), and has relatively spared motion processing, because the motion sensitive area MT+ is spared in both hemispheres (Arcaro et al., submitted; Culham et al., 2008). Previous neuroimaging work with MC has revealed that her lateral occipital cortex (LOC) – which is critical for visual object recognition (James, Culham, Humphrey, Milner, & Goodale, 2003; Malach et al., 1995) – is damaged in both hemispheres (Culham et al., 2008; Snow et al., 2015). In addition, MC demonstrates no BOLD activation for either static or moving faces within the expected coordinates of the fusiform face area (FFA), occipital face area (OFA) or the superior temporal sulcus (STS) (Culham et al., 2008; J. Culham, personal communication, June 9, 2017). Figure 1a depicts a lesion map for patient MC presented in Talairach space on a high-resolution (i.e., 1mm ISO-voxel) T1 MRI scan (for details concerning the imaging parameters and lesion mapping see Wood et al., 2016). For high-resolution T1 MRI images of patient MC's brain without the lesion overlay, see Supplementary Figure 1. Figure 1b presents crosshairs on the same lesion trace to depict the average coordinates (in Talairach space) of well-known face processing regions in the "core" face processing system which encompasses the

OFA, the FFA, and the STS (Gobbini & Haxby, 2007; Haxby, Hoffman, & Gobbini, 2000). Approximate locations for these regions were calculated using activation maps generated by the Neurosynth database (http://neurosynth.org/) (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) using the search term "face". The resulting meta-analysis activation map was based on 720 published fMRI studies. From this activation map we then extracted the MNI coordinates (which were then translated into Talairach coordinates) that corresponded to the centre of the activation cluster for the OFA, FFA, and STS (Table 1). Based on this analysis it is clear that the OFA appears to be completely damaged in both hemispheres whereas the FFA appears to be partially if not completely damaged in both hemispheres. The portion of the STS that is responsive to faces in healthy adults appears to be structurally intact in MC in both hemispheres. Finally, it is important to note that the anterior temporal lobes and amygdala (part of the "extended" face processing network) are undamaged bilaterally.

-- insert Figure 1 here --

--insert Table 1 here—

Before the experimental testing began a consent form was read aloud to patient MC where she then provided written informed consent. All experimental procedures were approved by the University of Western Ontario Health Sciences Research Ethics Board.

2.1.2 Control participants

In addition to examining face, gender, and target localization performance in patient MC, we also collected data on the same tasks in a group of young controls (n=26, mean age=20.62 years;

SD=1.65; 17 females, all right handed), and one age-appropriate and gender matched control (a right handed 43-year-old female). All participants provided written informed consent prior to testing. Young controls received course credit for participating. The age-appropriate control was a volunteer from the university community, and did not receive compensation. All experimental procedures were approved by the MacEwan University Research Ethics Board, as well as the University of Alberta Health Sciences Research Ethics Board.

2.2 Experimental tasks.

2.2.1 Stimuli for face processing tasks.

All face stimuli for both the gender and emotion discrimination tasks were taken from the NimStim emotional faces database (Tottenham et al., 2009). From the database, we selected an equal number of male and female actors (18 each) depicting neutral (for the gender discrimination task) as well as happy, fearful, and angry emotions. Photos from the same actors were used in each of the tasks. All images were black and white photos presented in the center of the screen at 500 x 650 resolution for unlimited duration until a response was given from the participant.

Given that MC is completely blind for static stimuli, it was challenging to get her to fixate in a specific location prior to each trial. The solution to this was to present a fixation point she could readily report. For this, we relied on MC's spared motion processing (Arcaro et al., submitted; Culham et al., 2008; Dutton, 2003) and used a 3cm square black and white reversing (4Hz) checkboard stimulus in the center of the screen for 1.5 sec prior to each trial of each task. This way, MC was able to locate the reversing checkerboard on each trial and focus her eyes on this location (as best she could). Following the 1.5 sec reversing checkerboard stimulus a random

delay of 1-2.5 s was inserted, followed by the simultaneous presentation of a 1000Hz auditory tone and the face. The auditory tone was used to indicate to MC that a stimulus had been presented, and that she was to guess, as quickly and accurately as possible, the gender or emotion of the face in the face discrimination tasks.

2.2.2 Gender discrimination task.

For the gender discrimination task, the faces of the 18 male and 18 female actors depicting neutral emotions were presented twice each for a total of 72 trials. Following the presentation of each face MC (and the controls) were to indicate, as quickly and accurately as possible, whether the face presented was male or female. Controls indicated their answer by pressing the left mouse button for "male" and the right mouse button for "female." Given that patient MC was completely blind, she indicated her "guess" as to the gender of the face verbally, and her response was input by the experimenter.

2.2.3 Emotion discrimination tasks.

For the emotion discrimination tasks, we selected emotional facial expressions that are at opposite ends of the emotional continuum, because we felt this would give MC the best chance of discriminating between them. Thus, we selected happy, fearful, and angry expressions. Furthermore, we used the same actors that were presented in the gender discrimination task. This was done to maximize the comparability of the gender and emotion discrimination tasks.

Each actor's face (18 male, 18 female) was presented once for each emotion (either happy vs. fear or happy vs. angry) for a total of 72 trials in each task. In one of the tasks MC (and controls) had to indicate whether the presented face depicted a "happy" or "fearful"

emotion. Controls indicated this by clicking the left mouse button for “happy” and the right mouse button for “fearful.” Again, MC indicated her guess verbally, and the experimenter recorded her response. In a modified version of this task, MC was re-tested with the same happy vs. fearful faces and asked to provide a confidence judgement after each trial ranging from 1 “no confidence at all” and 5 being “absolutely sure.” This was done to determine whether MC had any awareness or insight into her performance. The same experimental setup was used for the second emotion discrimination task in which MC (and controls) had to indicate whether the presented facial expression was “happy” or “angry”. However, confidence ratings were not required for this second task.

2.2.4 Target localization task

For the localization task we used a four-alternative forced-choice procedure in which participants had to indicate the location of a large circle (5cm in diameter) relative to a centrally-presented fixation (above, below, left, or right). The distance from the fixation point to the centre of each circle was 7°. Targets appeared at each of the four locations with equal probability in a random order. All circles were white and were presented on a black background in order to maximize contrast in an attempt to facilitate MC’s ability to report them. The central fixation point was the same black and white reversing (4Hz) checkboard stimulus used in the affective discrimination tasks. The fixation stimulus was presented in the center of the screen for 1.5 s. Following the presentation of the fixation stimulus, a random delay of 1-2.5 s was inserted prior to the onset of the circular target for 200 ms which was paired with the presentation of a 1000Hz auditory tone. Following the presentation of the target (signaled by the tone) the participant indicated their answer. MC indicated her answer verbally, and this was recorded by the experimenter. Controls

indicated their answer by pressing the up, down, left, or right arrow on the computer keyboard. The localization task was run in blocks of 20 trials (five in each of the four locations). MC was tested with four blocks (i.e., 80 total trials), whereas controls completed a total of two blocks (i.e., 40 trials).

2.3 Procedure.

2.3.1 Testing procedures for patient MC.

In the current study patient MC completed the four different experimental tasks over three days during the same week in the following order: Day 1: 1st half (i.e., 36 trials) of the gender discrimination task, followed by the happy vs. fearful emotion discrimination task; Day 2: Happy vs. fearful discrimination task with confidence ratings (see Experimental Tasks above), followed by the happy vs. angry emotion discrimination task; Day 3: 2nd half of the gender discrimination task (i.e., another 36 trials), followed by the four-alternative forced choice target localization task.

For patient MC stimuli for all tasks were presented on a 15" LCD monitor (60Hz refresh) at 1024 x 768 resolution at a viewing distance of 57cm in a dimly lit room. MC sat in front of the monitor with her head in a chin rest in order to restrict head movement and limit the possibility of creating self-generated motion cues. Prior to the start of each task, MC was informed of the probability of each stimulus occurring (50% for the gender and emotion tasks, 25% for the localization task) as well as the stimulus categories (i.e., male/female, happy/angry, etc.). MC was not provided with any feedback about her performance for any of the tasks.

2.3.2 Testing procedures for controls.

Younger controls and the age-matched control were tested in a different location. For controls, stimuli for all tasks were presented on a 24" widescreen LCD monitor (60Hz refresh) at 1920 x 1080 resolution at a viewing distance of 57cm in a dimly lit room. The stimuli and procedures for controls were generally the same as for patient MC (described above) except that no chin rest was used as head motion was not a concern, and all controls were tested in a single experimental session lasting approximately 45min. In addition, controls were not asked to provide any confidence ratings for their responses in the emotional discrimination tasks. Controls completed the four experimental tasks in the same order as patient MC: 1) gender discrimination task, 2) happy vs. fearful emotion discrimination, 3) happy vs. angry emotion discrimination, 4) target localization task. We chose not to counterbalance the order of the experimental tasks in controls because MC was only able to be tested using one specific task order. Given that it was only possible to test MC in one order, we wanted to keep this consistent in our control group as well.

Data analysis

Percent correct was calculated for the gender, affective, and target localization tasks for MC as well as the younger controls, and the age-appropriate control. To determine whether MC's performance was significantly better than chance for the gender and emotion discrimination tasks, as well as the target localization task, we used binomial tests (two-tailed). To determine whether younger control performance was better than chance for each of the tasks we used one-sample t-tests. Finally, to compare the performance of MC as well as the age-appropriate control to the younger control group's performance we used a modified independent samples t-test developed by Crawford and colleagues (Crawford & Garthwaite, 2002; Crawford & Howell,

1998) that compares the mean performance of a single-case to a control group using the standard deviation from control group. All reported *p* values are two-tailed.

Results

Control performance

Not surprisingly, performance of the younger controls (n=26) was near ceiling in each of the tasks (Figure 2). Specifically, performance of the younger controls was significantly better than chance (i.e., 50%) for the gender discrimination task (98.71; SD=1.37%; $t(25)=181.84$, $p<.0001$), as well as the happy vs. fearful (97.36%; SD=2.68; $t(25)=90.10$, $p<.0001$) and happy vs. angry (97.22%; SD=2.72; $t(25)=88.42$, $p<.0001$) emotional discrimination tasks. Finally, younger controls also performed better than chance (i.e., 25%) on the four-alternative forced-choice target localization task (99.04%; SD=1.88; $t(25)=200.68$, $p<.0001$).

Similarly, the age-appropriate and gender matched control also performed extremely well on all four tasks. Specifically, she scored 100% on the gender discrimination task, 98.6% on the happy vs. fearful faces task, 97.2% on the happy vs. angry faces task, and 100% on the target localization task. When we compared the age-appropriate and gender matched control's performance to that of the younger control group using the modified t-test procedure described above (Crawford & Garthwaite, 2002; Crawford & Howell, 1998) it revealed, perhaps unsurprisingly, that her performance was no different from that of the younger controls (all *p*'s >.10). Thus, for the sake of simplicity, we combined the age-appropriate control's data with that of the younger controls, to make a single control group (n=27) with which to compare to patient MC's performance (Figure 2).

Patient MC

Generally speaking, MC understood the task instructions and confirmed that she could see the reversing checkboard fixation stimulus in the centre of the screen. Thus, it seems reasonable to assume that she was fixating at the center of the screen when images were presented.

During each task she routinely insisted that, aside from the fixation stimulus, she "saw nothing" and was "completely guessing." This is consistent with previous observations that MC is completely blind for static stimuli. For each of the face discrimination tasks we analyzed MC's performance using binomial tests with .50 as the probability for success on a given trial. For the gender discrimination test (using combined data from Day 1 and Day 3), patient MC scored 38/72=53% (p=.72, two-tailed) which meant that she performed at chance (Figure 2). However, when MC was tested on the happy vs. fearful faces on Day 1 she performed significantly *above* chance scoring 48/72=67% (p=.006; Figure 2).

On Day 2 MC was re-tested with the same happy vs. fearful faces, however, she was also asked to subjectively rate her confidence on each trial using a 5-point scale (see Methods). When MC was asked to provide confidence ratings on each trial her performance for the same faces fell to chance levels, scoring 31/72=43% (p=.29; Figure 2). In addition, her confidence ratings were never greater than 2 on the five-point scale. We suspected that, by asking MC to slow down between trials and introspect on her answers, it may have disrupted her more automatic tendency to answer quickly with her initial "gut" choice. Thus, to further confirm that MC was truly able to discriminate emotions from faces we tested her again, this time using the happy vs. angry faces, without asking her for confidence ratings. Critically, MC once again performed better than chance scoring 46/72=64% (p=.025; Figure 2).

--insert Figure 2 here--

On Day 3 we tested MC's ability to localize targets using a four-alternative forced-choice procedure. To analyze MC's performance on this task we used a binomial test with .25 as the probability for success on a given trial. For this task MC performed at chance, scoring 23/80=29% (p=.51).

Finally, we compared MC's performance for the emotional face discrimination tasks to that of controls using the modified t-test procedure developed by Crawford and colleagues (Crawford & Garthwaite, 2002; Crawford & Howell, 1998). Although MC scored above chance on both the happy vs. fearful (67%) and the happy vs. angry (64%) emotional face discrimination tasks, she was significantly poorer than controls at the same tasks (both p's <.0001).

Discussion

In the current study, we examined gender and affective face discrimination performance, as well as target localization, in MC – a patient who has extensive bilateral lesions to occipital and ventral-temporal cortex (Figure 1). MC is completely blind to static stimuli (Dutton, 2003; Thaler et al., 2016), however, she has some spared motion perception abilities as the motion sensitive area MT+ is spared bilaterally (Arcaro et al., submitted; Culham et al., 2008; Dutton, 2003).

Data from the current study demonstrate that, using forced-choice procedures, MC was no better than chance at determining the gender of faces (Figure 2), or at localizing targets. However, MC was significantly better than chance when discriminating determining between happy and fearful, and happy and angry facial expressions. Importantly, MC denied ever seeing

any faces and insisted that she was "completely guessing" during the task. The notion that MC was unable to "see" the faces is further supported by the fact that she performed at chance for the gender discrimination task when pictures of the same actors were used (without emotional expressions). The fact that MC was able to perform above chance on emotion discrimination tasks without being able to consciously perceive a face is clear evidence that she possesses affective blindsight.

Taken together, these data constitute a replication of an important study by Pegna et al. (2005) in which they demonstrated a similar dissociation between preserved affective discrimination, but impaired gender discrimination in patient TN who (similar to patient MC in the current study) was left completely blind following bilateral damage to his occipital and ventral-temporal cortex. In addition to replicating Pegna et al.'s (2005) results, we also found that MC's ability to discriminate between facial emotions was impaired when she was asked to subjectively reflect upon her performance and provide a confidence judgment after each trial. This suggests that affective blindsight performance may be more likely to be detected when patients are encouraged to respond quickly and rapidly with their initial "gut" reaction to the stimulus, and are free from introspecting in the moment.

Although MC was able to reliably discriminate between different emotional facial expressions, given that we used faces from the same actors in each of the gender and emotion discrimination tasks, one could speculate that her performance was influenced by a learning effect. According to this line of reasoning, repeated exposures may have sensitized MC to these stimuli and aided her performance after some unspecified amount of time. We believe that MC's performance cannot be attributed to an effect of this sort for two reasons. First, we used a face stimulus set comprised from 36 different actors (18 male, 18 female) which makes an

explanation of this sort that is grounded in memory rather unlikely, especially given that she had no conscious vision of the faces. Second, a learning effect would predict an improvement in MC's performance over time. However, we did not observe this. On Day 1 MC was able to discriminate between happy vs. fearful faces, yet on Day 2 MC was unable to discriminate between the same set of happy vs. fearful faces when she was asked to give confidence ratings. If MC was becoming increasingly familiar with the faces then one would expect that her performance with the very same faces on Day 2 would have been reliable, or perhaps even improved, rather than at chance. Furthermore, MC's reliable performance for affective discrimination without confidence ratings did not improve from Day 1 (67% accuracy) to Day 2 (64% accuracy), again using the same actors. Finally, learning through exposure would have predicted improved performance on Day 3 when the same actors were once again used in the gender-discrimination task, yet MC performed at chance in this task.

The results we obtained with patient MC in the current study are similar to those reported in a recent study by Solca and colleagues (Solca, Guggisberg, Schnider, & Leemann, 2015) in which they investigated face discrimination in patient AM who was left completely cortically blind following bilateral strokes in the left occipital cortex and right occipital-parietal cortex. Similar to patient MC in the current study (and patient TN; Pegna et al., 2005), AM was able to discriminate between different facial emotions at above chance levels (i.e., 91% accuracy for fear vs. neutral), but was unable to discriminate between the gender of the presented faces. Surprisingly, AM was also able to discriminate between familiar and unfamiliar faces (93% accuracy), and he was able to correctly categorize famous faces according to occupation (i.e., actor vs. politician vs. athlete; 75% accuracy). However, AM was unable to overtly recognize any of the faces, was unable to discriminate between animals vs. shapes, and presented with no

other symptoms that are commonly observed in blindsight (e.g., shape discrimination, motion discrimination, etc.). Given AM's spared ability to discriminate between different faces, and facial emotions, Solca and colleagues (2015) proposed the term "facial blindsight" to describe his spared abilities.

Solca et al.'s (2015) results are surprising for two reasons. First, in many of the face processing tasks AM was not just above chance, he was near ceiling (75-93% accuracy), which is much more accurate than any other affective blindsight patient studied to date (at least to our knowledge). Second, the fact that AM could not only discriminate between familiar and unfamiliar faces, but also correctly categorize the faces according to occupation, suggests that AM was covertly processing the *identity* of the individual faces. AM's performance in face processing tasks is quite similar to descriptions of "covert face processing" in individuals with acquired prosopagnosia in which patients are unable to identify a face overtly, but may retain the ability to discriminate between familiar/famous vs. unfamiliar/non-famous faces, and may be able to sort faces according to different semantic categories (for reviews see Barton, 2008; Schweinberger & Burton, 2003). That AM retained these rather complex covert face processing abilities is likely explained by the fact that both the core (i.e., OFA, FFA, STS) and extended (i.e., amygdala, anterior temporal cortex) regions of the face processing network are undamaged bilaterally. For comparison, the FFA and OFA are damaged bilaterally in MC. It is also noteworthy that even though AM was completely blind, the occipital pole, and much of the tissue surrounding the calcarine sulcus in the right hemisphere, appears structurally intact. Unfortunately, no visual field testing was able to be conducted with AM, and no neuroimaging, or visual evoked potential data were collected. Thus, it is impossible to know whether spared regions of V1 in the right hemisphere, or other areas in the face processing network were

engaged during their face discrimination tasks. Nevertheless, these fascinating results indicate that it may be possible to demonstrate some degree of covert face recognition, even in the absence of conscious vision.

One important question that remains unanswered in the affective blindsight literature concerns the neural pathways that allow affective blindsight to occur. A good deal of behavioural and neuroimaging evidence supports the notion that the amygdala – a structure which is undamaged in MC – plays a critical role in the non-conscious (as well as conscious) processing of facial emotions (for reviews see Diano, Celeghin, Bagnis, & Tamietto, 2016; Pessoa & Adolphs, 2010; Tamietto & de Gelder, 2010). Although significant amygdala activation has been demonstrated in both healthy adults (e.g., Morris et al., 1999; Whalen et al., 1998), as well as patients with affective blindsight (e.g., Morris et al., 2001; Pegna et al., 2005) during the non-conscious processing of emotions, it is still unclear which specific pathways provide information to the amygdala to assist it in performing this function.

One popular theory suggests that the fast-automatic interpretation of emotional signals is served by a subcortical pathway through which retinal inputs to the superior colliculus are sent to the pulvinar nucleus of the thalamus which are then relayed directly to the amygdala, bypassing the cortex entirely (for reviews see Celeghin et al., 2015; Diano et al., 2016; Pessoa & Adolphs, 2010; Tamietto & de Gelder, 2010). However, critics of the so called "low-road" hypothesis have argued that there is limited anatomical evidence for the existence of this visual pathway in primates (for a review see Pessoa & Adolphs, 2010). Specifically, as reviewed by Pessoa and Adolphs, the inferior pulvinar receives inputs from the superior colliculus. However, the inferior pulvinar is strongly connected with visual cortex, not with the amygdala. Instead, the amygdala receives input from the medial pulvinar which is highly interconnected with a number of

different cortical structures, including those at various levels of the ventral stream hierarchy (e.g., Amaral, Behniea, & Kelly, 2003; Freese & Amaral, 2005; Iwai & Yukie, 1987). Finally, Pessoa and Adolphs note that activation in the amygdala does not appear to precede activation in the visual cortex and, therefore, the amygdala is unlikely to be a feedforward driver of the emotional content of visual stimuli in visual cortex. In short, the evidence does not favour a single "low-road" pathway for the rapid automatic appraisal of visual emotional signals in the absence of awareness. On the other hand, the evidence strongly suggests that the evaluation of visual emotional signals (both conscious and non-conscious) takes place via processing in a number of parallel pathways that involve input from both cortical and subcortical regions which include the amygdala and pulvinar (Pessoa & Adolphs, 2010).

The current study has some important implications for the proposal that affective blindsight arises via input from processing in both cortical and subcortical pathways. Specifically, MC has extensive bilateral lesions to the occipital and ventral-temporal cortex that encompass the lateral occipital cortex (Snow et al., 2015), the OFA, and at least part (if not all) of the FFA (Figure 1). In addition, as was mentioned previously, neuroimaging work with MC found no face selective activation in regions of the "core" face network (i.e., OFA, FFA, STS) (Culham et al., 2008; J. Culham, personal communication, June 9, 2017). Given these data, one can conclude that it is possible to demonstrate affective blindsight for discriminating facial expressions without any input from face processing regions within the ventral visual stream. Thus, any cortical inputs that might be required for affective blindsight to arise must come from other brain regions. Given the aforementioned considerations, we speculate that the amygdala, in concert with MC's spared regions in the temporal cortex, may underlie the visual analysis responsible for her affective blindsight.

Conclusion:

In conclusion, the current study adds to the growing literature on affective blindsight which indicates that it possible for a patient to discriminate between facial emotions in a blind visual field. In addition, the current data also demonstrate that affective blindsight may be more easily detectable when patients are encouraged to respond quickly and rapidly, as MC's performance fell to chance when she was asked to provide subjective confidence ratings about her performance. Finally, given that MC's lesions encompass brain regions that are critical for object (area LOC) and face recognition (areas OFA and FFA), we conclude that input from these areas are not necessary to observe affective blindsight.

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Table 1. Presents the average Talairach coordinates for the occipital face area (OFA), the fusiform face area (FFA) and face responsive region in the superior temporal sulcus (STS) in the left and right hemispheres. Coordinates were acquired from a meta-analysis of 720 published fMRI studies using the Neurosynth database (http://neurosynth.org/). These coordinates were then used to estimate the locations of these regions in patient MC's brain.

Region	**X**	**Y**	**Z**	**Brodmann area**
left OFA	-40	-81	-5	BA 19, extrastriate cortex
right OFA	43	-76	-5	BA 19, extrastriate cortex
left FFA	-39	-51	-13	BA 37, fusiform gyrus
right FFA	41	-51	12	BA 37, fusiform gyrus
left STS	-54	-51	11	BA 39, angular gyrus
right STS	53	-45	13	BA 39, angular gyrus

Figure 1. Panel A depicts patient MC's lesion mapped on to a high-resolution (1mm ISO-voxel) T1 MRI scan (for details see Wood et al., 2016). Images are presented in the axial plane in neurological convention (i.e., left is presented on the left). It is clear from the images that MC has extensive damage to occipital as well as ventral temporal cortex in both hemispheres. In addition, MC has a lesion to her right posterior parietal cortex. For MRI images of MC's lesion without the lesion trace, see Supplementary Figure 1. **Panel B** depicts the approximate locations (using crosshairs) of the "core" regions of the face processing network in the left and right hemispheres (see Methods). OFA=occipital face area, FFA=fusiform face area, STS= superior temporal sulcus. From the images it is apparent that MC has damage to the OFA as well as the FFA in both hemispheres; however, the STS appears to be anatomically spared in both hemispheres.

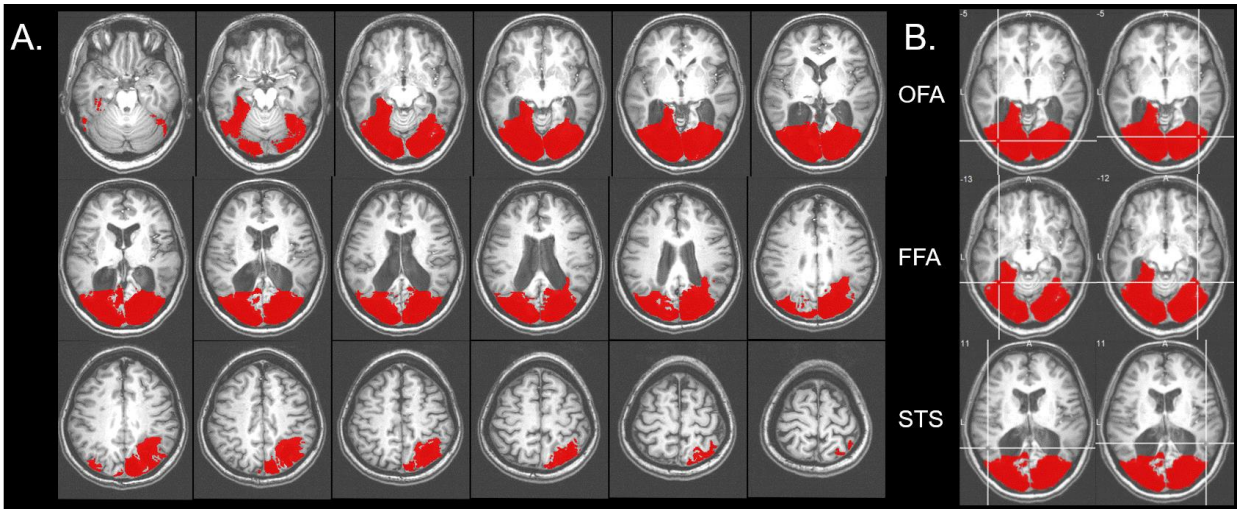
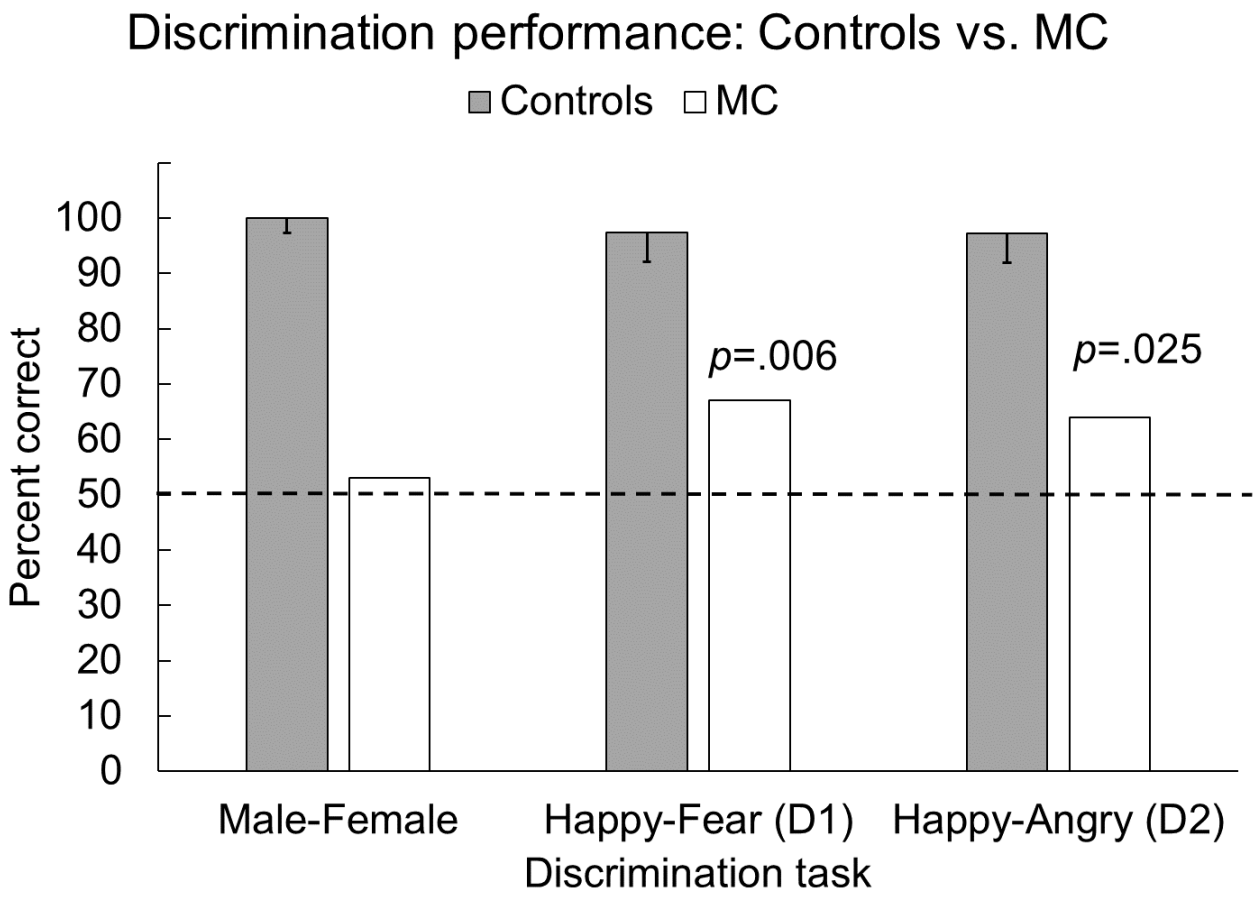


Figure 2. Depicts the accuracy data for controls (grey bars; n=27) as well as patient MC (white bars) for the gender and affective discrimination tasks. The dashed line represents chance performance. Error bars represent 2SD below the mean for controls. D1 and D2 indicate which tasks were completed on Day 1 and which were completed on Day 2. Critically, although patient MC is at chance for gender discrimination, she is significantly better than chance at discriminating between happy vs. fearful and happy vs. angry emotional expressions.



Supplementary Figure 1. Depicts high-resolution T1 MRI images of patient MC's brain. Images are presented in the axial plane in neurological convention (i.e., left is presented on the left). It is clear from the images that MC has extensive damage to occipital as well as ventral temporal cortex in both hemispheres. In addition, MC has a lesion to her right posterior parietal cortex.