Anosognosia for hemiplegia as a global deficit in motor awareness: Evidence from the non-paralysed limb

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ABSTRACT

The current study adds to the growing empirical research into the mechanisms underlying unawareness of paralysis following stroke (anosognosia for hemiplegia or AHP) by investigating action awareness for the non-paralysed limb in a single AHP patient. Visual feedback representing patient GC’s goal-directed reaching movements was either modified by a computer or left unperturbed. Unlike healthy and brain-damaged controls, GC was unable to detect computer-generated visual perturbations as large as 20°. GC also failed to report awareness of the large on-line corrective movements that he made when compensating (often unsuccessfully) for the visual perturbations. These results suggest that the motor comparators implicated in AHP are functioning, but not at optimum levels. Moreover, because the current findings reveal a deficit in awareness for reaches with the unimpaired limb, it is suggestive of common right hemisphere networks for motor awareness in both limbs and that AHP may be a global deficit in motor awareness as opposed to a specific lack of awareness for a particular motor deficit.

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1. Introduction

The past decade has seen remarkable growth in our understanding of the way in which we move and interact with the world around us. This subject is not only central to identifying the mechanisms responsible for our own actions, but provides considerable insight into how we interpret the intentions and desires of other people (Blakemore & Decety, 2001; Blakemore, Winston, & Frith, 2004). These abilities are fundamental to human social interaction.

A driving force behind recent discoveries has been the development of a computational ‘forward’ or ‘comparator’ model of motor control, based on well-established engineering principles (Miall & Wolpert, 1996). According to this model, the control and awareness of movement relies on the comparison of information derived from various sources (see Fig. 1).

Provided that we reach our desired state, such comparisons typically occur with limited conscious awareness (Fournet & Jeannerod, 1998). The comparisons are thought to serve several crucial functions, such as allowing the continual fine-tuning of movements during their planning and execution, detecting when errors in movement occur, and correctly discriminating our own actions (self) from those of another person (other) (Wolpert, 1997). These proposals are supported by the evidence from healthy and brain-injured populations using behavioural experiments (e.g. Blakemore, Frith, & Wolpert, 1999), functional neuroimaging (e.g.m), cortical stimulation/disruption (e.g. Preston & Newport, 2008a) and neuropsychological data (Fotopoulou et al., 2008; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010). However, the exact number, functions, and underlying brain mechanisms of the comparators remains equivocal.

Patients with abnormal motor awareness provide a unique opportunity to cast light on these unresolved issues. In particular, stroke patients who are not aware of severe motor impairments (i.e. patients with anosognosia for hemiplegia, or AHP) can help us to better understand the functional neuroanatomy of motor awareness. Recent forward/comparator model accounts of AHP suggest that the underlying cause of the disorder is a failure to detect discrepancies between patients’ predicted and (estimated) actual state (Berti & Pia, 2006; Frith, Blakemore, & Wolpert, 2000). Erroneous claims that the patient can move their paralysed limb are believed to occur because awareness in AHP is constructed entirely from intact predictions of intended movement (Fotopoulou et al., 2008; Jenkinson, Edelstyn, & Ellis, 2009)). Such discrepancies usually trigger the mechanism responsible for conscious awareness and self-correction of the error (Fournet & Jeannerod, 1998); however, AHP seems to represent an instance of pathological (lesion-induced) unawareness of large discrepancies between the predicted and actual state of the body, such that normal monitoring.
is impaired and awareness is deceived (Jenkinson & Fotopoulou, 2010).

Accounts of AHP disagree on the source of this failure to detect errors. Frith et al. (2000) propose impaired input to the comparators responsible for monitoring concordance of the estimated actual states of the limb with the predicted and desired states. Alternatively, Berti and Pia (2006) suggest that the actual vs. predicted states comparator itself is damaged with the main distinction between the two theories being the certainty with which the comparator is held responsible (see Fig. 1 and Jenkinson & Fotopoulou, 2010 for further discussion of this point). However, no study to date has directly assessed the functionality of the comparator(s) in AHP. What is more, the suggestion of an impaired motor comparator may not be so straightforward. The observed specificity of AHP (e.g. differential perceived abilities for the arm and leg within patients; Marcel, Tegner, & Nimmo-Smith, 2004), and apparent independence of verbal/behavioural (Jehkonen, Laihosalo, & Kettunen, 2006) or implicit/explicit awareness (Cocchini, Beschin, Fotopoulou, & Della Sala, 2010) suggests that certain comparators may be impaired in AHP, while others remain intact. Furthermore, reports of AHP following unilateral left-hemisphere lesions (Cocchini, Beschin, Cameron, Fotopoulou, & Della Sala, 2009) argue against explanations that have located the mechanisms responsible for conscious error detection exclusively in the right hemisphere (e.g. Preston & Newport, 2008b; Ramachandran, 1995). More experiments are needed to further investigate these unresolved issues.

Observations in patients with AHP, such as those described above, have been useful in providing insight into the workings of the healthy motor system; however, they present only indirect evidence regarding the possible operation of comparator mechanisms. The current experiment directly explores the functioning of the motor comparator(s) in a case of chronic AHP, primarily using a movement agency task to assess the patient’s ability to detect and correct movement errors, by examining the performance using the unimpaired limb. AHP performance was compared with that of a group of hemiplegic patients without anosognosia (patient controls), and young healthy controls. The task involved making self-other judgements about observed reaching movements involving the intact (non-hemiplegic) hand, during which the participants received visual feedback of a visually coincident cursor that was spatially perturbed or unperturbed. The ability to detect discrepancies was assessed by asking the participants to state whether the movement seen was self (unperturbed) or other (perturbed). Furthermore, kinematic data regarding the participants’ movement trajectory was used to objectively assess reach accuracy and on-line correction.

If damage to a general right-hemisphere motor comparator is responsible for impaired awareness in AHP, then self-other judgements should be selectively disrupted in the AHP patient regardless of which arm was involved in reaching. That is, if awareness of motor actions for both the left and right hands predominantly involves a right hemisphere network (e.g. Preston & Newport, 2008a, 2008b; Ramachandran, 1995), then damage to this network should also have implications for awareness of movements performed by the non-paralysed limb and should not be restricted to the paralysed contralesional limb for which the patient exhibits anosognosia. Furthermore, selective impairment of the comparator that provides information for high-level monitoring of self-other judgements might spare other low-level comparators responsible for the automatic updating and correction of movement errors, in which case subjective self-other judgements and reach accuracy measures should dissociate. The current study considered both of these measures in order to tease apart the different components of motor awareness.

2. Methods

2.1. Subjects

2.1.1. AHP patient

Patient GG was a 64-year-old right-handed male who suffered an extensive right-hemisphere frontoparietal haemorrhage focused at the level of the lentiform nucleus 1 year prior to testing (Fig. 2). GG’s brain damage resulted in unilateral visual neglect and left-sided hemiplegia such that he had no volitional movement in his left arm or left leg (power = 0; Medical Research Council scale). On examination of his intact right arm GG was found to have no significant motor deficit (power = 5; Medical Research Council scale) and, while he was poor at two point discrimination, he appeared to have preserved position sense (for example, he was able, with his eyes closed, to point accurately to targets on both sides of his body and to accurately detect small, passive changes in limb posture). No significant cognitive impairment was identified using the mini mental state examination (MMSE, Folstein, Folstein, & McHugh, 1975). GG also suffered from chronic anosognosia for his left-sided hemiplegia, as demonstrated by frequent spontaneous comments that suggested impaired awareness regarding his injuries. The most striking of these involved aspects of gardening which, given his dense hemiplegia and wheelchair/carer dependence, were clearly beyond his capabilities. For example, GG was noted as saying “I think I am going to move the lettuces nearer to the house so that we don’t have to walk as far to get to them” and “This year I am going to build a cold frame for the garden”. GG also lives in a residential home due to his ongoing hemiplegia, but when asked why he had to live there he reported that it was due to his wife being unwell, although he sometimes referred to the home as a hospital and he now admits that he has had a stroke. In addition to these informal measures, GG’s anosognosia was confirmed by formally assessing his awareness (or lack thereof) when asked directly about his injuries (Marcel et al., 2004, see below). GG was also unaware of his visual neglect and neither did he spontaneously mention anything wrong with his vision or attempt to employ strategies on clinical tests for neglect.

2.1.2. Upper limb awareness

Although GG reported some problems with his left hand such as limited movement and pain they were greatly understated. In the verbal assessment of his upper limb paralysis he claimed to have movement in his left arm (in fact, GG had no volitional movement of his left hand) but refused to attempt to point with it claiming “This year I am going to build a cold frame for the garden” and “This year I am going to move the lettuces nearer to the house so that we don’t have to walk as far to get to them” and “This year I am going to build a cold frame for the garden”.

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of 5/10, ranging from 0/10 for eating with a fork using his left hand to 10/10 for clapping. It should be noted that for scores lower than 5, and for some lower than 10, he always gave a confabulatory explanation. For example, the score of zero for eating with a fork was accompanied by the statement, “I don’t know. I haven’t really tried that, so I had better give it a zero.”

2.1.3. Lower limb awareness
When asked “how is your left leg” GG stated that it was “showing improvement” and although he reported having pain in his left leg and admitted limited movement (there is no volitional movement of his left leg) he stated that he could walk with no problems (i.e. severe AHP according to the AHP assessment of verbal awareness of
the lower limbs, Berti, Ladavas, & Della Corte, 1996). In addition to walking, when asked to rate his ability to perform other activities such as driving and jumping he gave a median score of 6/10 ranging from 0/10 for riding a bicycle to 10/10 for walking and note. That here also for all activities that GG gave a less than optimal score, he attributed his inability to not having done them recently. For example, he rated his ability to ride a bicycle as 0/10, not because of his paralysis, but because he had not ridden since he was a child and would probably fall off.

2.1.4. Patient control group

A control group of 4 stroke patients (1 female, 3 male) participated in the study with a mean age of 67 (range 50–82). All patients were pre-morbidly right hand dominant and had right-hemisphere lesions that resulted in left sided hemiparesis/hemiplegia and all had visual neglect. As a selection criterion, all control patients were assessed for AHP and were found to be fully aware of their motor deficit, all scoring 9 (normal awareness) in a verbal assessment of both upper and lower limb awareness and when rating ability in performing specific actions using the impaired left limb their scores accurately reflected their actual abilities (mean = 0.8/10 for left handed actions, mean = 1.3/10 for bimanual actions). The patients were also screened for severe cognitive impairment using the MMSE and, despite 2 patients scoring only 17/30, all could understand the task instructions and perform the task successfully. Each of the patients gave fully informed consent prior to taking part in the study (see Table 1 for patient demographics). Crawford and Garthwaite’s (2002) modified t test revealed no significant differences between GG and the patient control group on any of the demographic measures taken (minimum p value = 0.53).

2.1.5. Young control group

Eight healthy young controls took part in the study (1 male) with a mean age of 26 years (range = 21–29 years). All were right hand dominant with normal or corrected to normal vision. The purpose behind including a group of young healthy controls was to provide a framework of normal performance on this type of task unimpaired by age or brain injury.

3. Materials

Participants’ reaching movements were represented by the movements of a 20 mm white cursor that was projected, along with the target location, onto a horizontal semi-transparent screen positioned 450 mm above the reaching limb. Participants viewed the cursor via a horizontal mirror positioned equidistant between the limb and projection such that visual feedback of the participant’s movements appeared in the same spatial plane as the actual reaching limb (see Fig. 3). An advantage of having the visual feedback in the same plane as the movement is that it reduces, or indeed removes, the need for the computation of the additional sensorimotor transformations that would be required were the visual plane be perpendicular to, or detached from, the movement plane – as is often the case in such studies. In addition, it is more intuitive that the cursor represents the participant’s own hand when it can be viewed in the same plane as the actual hand. The location of the cursor was calculated on-line using position data recorded by a vBOT 2D robotic manipulandum sampling at 1000 Hz (see Howard, Ingram, & Wolpert, 2009 for a comprehensive description of this device).

4. Procedure

Participants sat looking down into the mirror and held onto the vBOT handle with their right hand. Before the beginning of each trial the vBOT moved the limb to a start location just out of view and directly in front of their midline. At the beginning of each trial a blue 30 mm circular target appeared for 500 ms at randomly varying locations averaging 210 mm forward from the start location. Target locations directly ahead of the midline were used due to some of the neglect group being unable to detect leftward targets. Immediately following the target disappearance a tone indicated that the participants should begin their reach. Visual feedback of the reaches (path of the cursor) was either an exact representation of the actual movement (self) or had an angular perturbation applied (other). Other actions were defined as actions that were not self-produced (i.e. not the same as the movement performed), as opposed to the actions of another human being. This was made clear to, and understood by, all participants.

The experiment consisted of 5 experimental blocks, each of which contained 20 trials (totalling 100 trials). In one-fifth of the trials, the position of the cursor was taken directly from the vBOT position (an exact representation of the participant’s actual movement). All other trials were equally divided between –8°, –4°, 4° and 8° perturbations (with negative values indicating a leftward perturbation). At the end of each reach participants were required to give a verbal self/other judgments as to whether the movements of the cursor represented their actual movement (self) or whether it had been modified by the computer (other). Due to GG’s inability to detect the perturbations, following just two blocks of the 4° and 8° perturbations he took part in a further two blocks using −12°, −6°, 6° and 12° and finally an additional four blocks using the perturbations −20°, −10°, 10° and 20°. In two of the blocks using perturbations of 10° and 20° the question was changed as an attempt to further verify that GG could not detect

Table 1

<table>
<thead>
<tr>
<th>Patient</th>
<th>NG</th>
<th>LS</th>
<th>KM</th>
<th>FA</th>
<th>GG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>50</td>
<td>82</td>
<td>57</td>
<td>80</td>
<td>63</td>
</tr>
<tr>
<td>Lesion site</td>
<td>Right temporoparietal CVA</td>
<td>Posterior aspect of the right temporal lobe extending to the right occipital lobe</td>
<td>Right temporal haematoma</td>
<td>Right parietal CVA involving the right frontal operculum and the head of the right caudate nucleus</td>
<td>Right frontoparietal haematoma</td>
</tr>
<tr>
<td>Time since stroke (months)</td>
<td>36</td>
<td>21</td>
<td>8</td>
<td>18</td>
<td>12</td>
</tr>
<tr>
<td>MMSE</td>
<td>23</td>
<td>17</td>
<td>29</td>
<td>17</td>
<td>26</td>
</tr>
<tr>
<td>NART</td>
<td>33/50</td>
<td>31/50</td>
<td>41/50</td>
<td>38/50</td>
<td>38/50</td>
</tr>
<tr>
<td>Verbal IQ (estimated)</td>
<td>Verbal IQ = 108</td>
<td>Verbal IQ = 106</td>
<td>Verbal IQ = 117</td>
<td>Verbal IQ = 114</td>
<td>Verbal IQ = 114</td>
</tr>
<tr>
<td>Verbal IQ (corrected)</td>
<td></td>
<td></td>
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</tbody>
</table>

![Fig. 3. Participants viewed a cursor representation of their hand via a horizontal mirror positioned equidistant between the limb and a projection screen such that visual feedback of the participant’s movements presented on the screen appeared in the same spatial plane as the actual reaching limb.](image-url)
the perturbations. In the first of these he was asked whether he had to make on-line motor corrections in order to reach the target (“did you have to correct?”), for which he made yes/no responses for having to correct or not correct, respectively. In the final block the question related to his perceived accuracy to the target (“was the cursor accurate?”), for which he made hit/miss responses for accurate and not accurate, respectively. Note that in the accuracy trials it was made clear to GG that judgments of reach accuracy were to be made in respect to the cursor and not to his actual limb. This research was approved by the University of Nottingham, School of Psychology Ethics Committee and conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

5. Results

5.1. Judgement data

Self/other judgments were converted into percent self-scores for each participant at each perturbation size. The overall pattern of responses for the healthy control participants exhibited a relatively normal distribution with the peak of self-responses being centred on 0° perturbations. This pattern of results corresponds well with the results of similar paradigms using this measurement method (Farrer, Bouchereau, Jeannerod, & Franck, 2008). GG, on the other hand, recorded a totally flat response profile, responding at 100% self for each perturbation size and falling outside the 95% confidence intervals calculated for both the healthy and neglect control groups for each perturbation (Fig. 4). For reaches with the larger perturbation sizes (only performed by GG), again, GG’s performance is clearly abnormal, responding with self-judgments on larger perturbation sizes (only performed by GG), again, GG’s performance is clearly abnormal, responding with self-judgments on larger perturbation sizes (only performed by GG), again, GG’s performance is clearly abnormal, responding with self-judgments on larger perturbation sizes (only performed by GG).

It is notable that the performance of the neglect patients appears to be skewed and shifted such that the peak for self-responses falls to the left of centre. This is not simply a group effect as each of the patients produced a similar performance. The pattern is consistent with theories of neglect based on a compression of space centred on 0° perturbations. If the visual representation of the limb in left space is remapped as being further rightward than its veridical position, then it might be perceived as being closer to the proprioceptively felt position of the limb than it really is—giving rise to an increase in self-judgements. Cursors appearing in central and right space, on the other hand, might be perceived as more rightward than the veridical position, potentially leading to a reduction in self-responses to zero and rightward perturbations.

5.2. Accuracy and correction judgements

GG was very accurate when reaching in unperturbed trials. Endpoint errors (calculated in the lateral × dimension measured from the seen cursor position, not the actual hand position) in this condition were very small (median absolute end point error = 1.9°), and smaller than all of the other patients (range of medians = 3.5–6.2°) including the reaches of the most closely matched patient control, KM (median = 3.5°). This demonstrates that his ability to integrate sensorimotor information in order to plan and execute reaches remained intact. Inspection of GG’s handpaths in the perturbed conditions, however, revealed that many of his reaches exhibited large and late on-line corrections. His errors across all perturbation sizes ranged from 0.03° to 24.94° with a median of 3.1° (the median error increased to 12.6° for the largest 20° perturbations). Note that an error of ~12° for the cursor in the 20° perturbation condition represents an error of 8° for the true position of the hand).

Despite these substantial inaccuracies, sometimes accompanied by very large corrective movements (see Fig. 5), GG rated his perception of reach accuracy as always being accurate (100% accurate responses) for all perturbations while his reporting of motor corrections remained fixed at 0% (never having to correct). Although it was not tested directly, these data would argue against an account positing that GG’s deficit was caused by a failure to successfully integrate visual and proprioceptive information regarding the limb. In any case, such impairment could only be in addition to, and not instead of, a failure to be aware of the consequences of his own reaching movements.

5.3. Kinematic data

The first two blocks of GG’s reaches were compared to those of control patient KM. Only the first 36 of KM’s reaches were used because 4 trials were lost from GG’s data due to GG letting go of the vBOT handle, causing early termination of the trial. The first two blocks were chosen because they could be directly matched for perturbation size and KM was chosen as the most closely matched of the control patients (in regards to age, cognitive score, physical disability). Paired samples t-tests demonstrated that the overall profile of reach kinematics were very similar between the two, with no significant differences found for peak velocity (t(35) = 0.26, p = 0.8) (GG mean = 336.2 mm/s, S.D = 79.5 mm/s; KM mean = 341.5 mm/s, S.D = 73.9 mm/s) or movement time (t(35) = 1.44, p = 0.16) (GG mean = 1280 ms, S.D = 210 ms; KM mean = 1200 ms, S.D = 220 ms).

Fig. 4. Patient GG’s mean % self-responses (crosses) plotted against the mean (and 95% confidence intervals) for young healthy controls (open circles) and elderly brain-damaged controls (filled squares) at each of the 0°, 4° and 8° perturbations.

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6. Discussion

These results demonstrate a clear dissociation between subjective self-reports of motor awareness and objective movements involving the unimpaired limb. Despite perturbations of up to 20° applied to his real movements, GG consistently reported that these observed reaches accurately represented his own actual reaches. GG’s judgements of movement agency are clearly abnormal, falling far outside the confidence intervals of both young healthy controls and age-matched patient controls. This, it must be stressed, is in relation to reaches made with his intact limb, whereas previous accounts of impaired motor awareness in AHP have concentrated on erroneous reports of action in the paralysed limb (with the exception of an anecdotal description by Ramachandran (1995) of a single patient, FD). As such, this experiment is unique in reporting empirical evidence of abnormal motor awareness for successfully executed actions in AHP.

External influences on actions are normally detected relatively easily by healthy controls, provided the perturbation is above around 5° (Farrer, Franck, Paillard, & Jeannerod, 2003), although unawareness of larger perturbations have been reported under particular experimental circumstances designed to reduce awareness (Michel, Pisella, Prablanc, Rode, & Rossetti, 2007; Preston & Newport, 2010). For this experimental manipulation healthy controls performed near chance for 4° perturbations and easily detected 8° perturbations to either side of the real movement. Instead of the typically observed normal distribution for self-reports, which is centred around zero (e.g. Farrer et al., 2008), GG’s judgements profile was totally flat. GG judged all reaches as self-produced, despite the cursor representing his hand being perturbed by up to 20° from his real hand, and missing the intended target area by an average of 11.95° (for the largest perturbation sizes). This remarkable behaviour demonstrates a clear deficit in detecting discrepancies between the estimated actual and predicted states of the arm, and provides strong evidence of a change in the efficiency of the comparator responsible for this function (see C3, Fig. 1).

In spite of his unawareness at a conscious level, GG’s motor system nevertheless frequently corrected his movements on-line (Fig. 5), particularly for the larger 10 and 20° perturbations. This suggests that the comparators thought to be responsible for movement control and accuracy (i.e. those between the actual estimated and desired states [C2], and predicted and desired state of the limb [C1]) are still functioning in GG. The performance of one or both of these comparators appears to be less than optimal, since all movement corrections were large and late (although it should be noted that the velocity profiles suggest that some of these are secondary movements, rather than corrective movements). The current results suggest that although these comparators receive appropriate input and are functional, their ability to update the controllers responsible for programming movements and making on-line corrections may be compromised. Furthermore, the errors detected by these comparators did not give rise to conscious awareness. GG claimed to be reaching accurately regardless of whether or not he made corrections suggesting that these comparators may not feed into consciousness, or that their usual role in this process is impaired. Minor, unconscious corrections have been observed experimentally, in healthy participants, using incremental adaptation (e.g. Michel et al., 2007) or double-step paradigms in which the target suddenly jumps to a new location (e.g. Goodale, Pélisson, & Prablanc, 1986), especially if this change occurs during a saccadic eye movement. The dissociation between GG’s corrective performance and lack of conscious awareness offers support for the putative existence of independent mechanisms for automatic, on-line correction and conscious control of movement (e.g. Pisella et al., 2000).

Despite the cursor being presented in the same plane as the actual hand, it could be argued that GG’s performance results from a problem integrating the seen position of the hand (the cursor) with the felt position of the hand and is thus unable to detect a discrepancy between the two. However, the data from unperturbed trials shows that GG is accurate, demonstrating his ability to integrate visual and proprioceptive signals; GG made corrections to his movements unconsciously, thereby, again, demonstrating this ability to integrate visual and proprioceptive information; if such a problem were related to his neglect then the control group would be expected to have the same problem, which they do not. This, therefore, cannot in itself explain the lack of motor awareness in the AHP patient.

A recent study by Jenkinson et al. (2009) investigated the functionality of the comparator that detects discrepancies between the desired and predicted state of the limb (C1) in AHP. This was achieved using the grip selection task that compares judgments of how patients state they would grasp a wooden rod (a task that necessitates mental rehearsal) with how they actually grasp it. Because our limbs are mirror images of each other, transposing results from the non-paralysed limb allows predictions to be made
about actual grasps with the hemiplegic limb. Jenkinson and colleagues found no difference in performance between AHP patients and matched patient controls without AHP. Both patient groups, however, showed a significant impairment on the task for both the hemiplegic and the non-paralysed limb and comparable results have been observed with GG in a modified version of this task. Improving motor control through mental rehearsal, and the fine-tuning of movements during their execution, is thought to be one of the major functions of the third comparator (C1 in Fig. 1). Therefore, the deficit observed for both AHP and non-AHP hemiplegic patients in the grip selection task provides support that the performance of comparator C1 is also disrupted. Importantly, because the deficit in performance was not exclusive to the AHP patient or to the hemiplegic limb it suggests that unawareness of paralysis in AHP cannot be explained by C1 disruption alone.

It is important to remember that while the overall purpose of the comparators is to maintain and improve motor control, because of inherent noise in the system (partially arising from delays in sensory transduction), the various comparators must allow a certain amount of leniency. Take, for example, the comparator that monitors concordance between the predicted and estimated actual state of the limb (C3, Fig. 1): if the threshold for judging movements as self-produced is too strict, then genuinely self-produced movements would be perceived as being not self-produced, or worse still, externally produced. The result would be a subjective sense that our movements are not our own, like that experienced by patients with delusions of control in schizophrenia (Synofzik et al., 2010). Such experiences severely compromise our ability to function effectively as social beings.

It is reasonable to expect that the discrepancy threshold for judging movements as self-produced should be at least as great as the inherent noise, thereby allowing normal and effective movements to pass unnoticed. The same may be true for the other comparators, particularly that comparing the estimated actual and the intended states (C2) and experimental examples of small corrections going unnoticed are frequently observed in double-step paradigms (e.g. Goodale et al., 1986). When the brain is damaged, it is likely to increase the level of noise in the motor system, which may be considerable following a stroke that results in hemiplegia. In order to deal with everyday movements in the presence of this increased noise, the comparators must therefore relax the threshold for signalling errors. The suggestion here is not that any of the comparators are necessarily broken in AHP, but that their parameters have been pathologically relaxed, to the extent that actual movements are treated as self-produced, even when they bear little resemblance to those intended.

This slackening of control is apparent to some extent in the current neglect group, for whom the criteria for self-movements appears to have been broadened. This suggestion is consistent with anecdotal reports that many neglect patients often fail to notice errors while undergoing prism adaptation procedure (Michel et al., 2007; Rode, Pisella, Rossetti, Farne, & Boisson, 2003). Healthy controls will typically and spontaneously make vocalisations reflecting surprise when failing to reach accurately towards a prism-displaced target, and will make conscious strategic corrective movements in order to become accurate. By contrast, neglect patients frequently fail to register surprise, can be unaware of the prism-induced error when explicitly asked, and are often slow to make strategic corrective movements (Michel et al., 2007). In the current study, however, GG’s performance cannot be explained simply by severity of neglect syndrome as he was far from being the worst in the group for all of the neglect measures recorded (cancellation tasks, line bisection and scene copying), yet all other patients demonstrated some ability to detect the perturbations (and it is worth noting here that we have not observed this level of impairment in any of the patients tested on similar paradigms in our lab).

Therefore, it is suggested here that in the case of anosognosia, the raising of the comparator thresholds is such that all movements are treated as both self-produced and accurate. Thus, when a movement is intended, and, importantly, a motor programme produced, the movement is treated as self-produced, even though no actual movement has taken place. This idea is compatible with the Frith et al. (2000) model, in which the comparators are working, but pertinent information fails to reach consciousness; nor is it incompatible with Pia and Pia (2006), as the comparators, while not broken, are not functioning normally.

A final implication of the present study relates to the neuropsychological basis of AHP and the motor comparators, which remain a matter of considerable debate. Pia, Neppi-Modona, Ricci, & Berti (2004) found that AHP was most frequent following combined damage to frontal and parietal areas, while AHP following purely subcortical lesions typically involved the basal ganglia and thalamus. Berti et al. (2005) found AHP to be associated with frontal areas responsible for programming movements (Brodmann areas 6 and 44), suggesting that the control and monitoring of movements may be implemented within the same neural circuitry (see also Spinazzola, Pia, Folegatti, Marchetti, & Berti, 2008). These findings are supported by evidence in healthy controls that the brain mechanisms responsible for motor awareness are located between the primary motor and premotor cortices (Haggard & Magno, 1999), and discrepancies between motor intention and sensory outcome activate right prefrontal cortex (Fink et al., 1999). Several other studies have also identified damage to the insula as a key occurrence in patients with impaired awareness (Baier & Karnath, 2008; Karnath, Baier, & Nägele, 2005; Spinazzola et al., 2008). Although the current study cannot draw any conclusions regarding the specific brain regions responsible for AHP or the motor comparators due to his extensive lesion, GG’s clear deficit in motor awareness for actions performed with his non-paralysed limb, in addition to AHP for his left sided paralysis, provides novel empirical evidence suggesting that the mechanisms for awareness of both left and right hand movements involve right hemisphere networks, an idea originally put forward by Ramachandran (1995). Whether the comparators for both limbs involve right hemisphere regions, or information produced by separate left and right hand comparators is fed into a single ‘conscious awareness detector’ located in the right hemisphere remains unclear and cannot be teased apart by GG’s 100% self-reports in the current study (i.e. it is possible that the left hand comparators are functioning normally, but the awareness module is damaged). However, GG’s impaired awareness for his right hand movements may suggest that AHP, rather than being a specific lack of awareness for a motor deficit, is actually a more global deficit for motor awareness. Of course, different within-patient levels of overestimation in the perceived motor abilities of the arm and the leg, despite both being similarly impaired, have been observed in patients with right brain damage (Marcel et al., 2004). For such cases a global deficit in motor awareness may seem fallacious. However, due to the different constraints of arm and foot movements it is reasonable to assume that they may be controlled by separate comparators, or at least separate comparator thresholds, which may, in turn suffer differing degrees of abnormal slackening following stroke dependent on lesion size and location. In any case, the key suggestion here is that anosognosia, rather than being a lack of awareness of paralysis per se, is a general deficit of motor awareness whether the limb(s) in question are paralysed or not.

In summary, the current results demonstrate dissociation between subjective and objective motor awareness of the non-paralysed limb in AHP. GG was able to perform low-level motor corrections to compensate for large visual perturbations, albeit poorly, that he was not consciously aware of, suggesting that forward model comparators implicated in AHP are not actually broken but that AHP may be a result of an abnormal slackening of normal
Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). Mini-mental state-practical


