VISUAL AFFORDANCES DIRECT ACTION: NEUROPSYCHOLOGICAL EVIDENCE FROM MANUAL INTERFERENCE

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We report an experimental study of the factors that elicit manual interference in a patient with so-called "anarchic hand" behaviour in everyday life (Della Sala, Marchetti, & Spinnler, 1991, 1994) due to corticobasilar degeneration. The patient, ES, showed problems with both hands. We used tests in which ES had to respond to a left-side object with her left hand and to a right-side object with her right hand; manual interference responses occurred when she used the left hand to respond to the right-side object and the right hand to respond to left-side objects. In reaching tasks, interference responses were determined by stimulus familiarity and by the spatial relations between the hand of response and the part of the object used for action (the handle of the cup). In pointing tasks interference responses were affected by both effector and spatial uncertainty. Right hand responses were affected particularly by familiarity, and left hand responses by effector and spatial uncertainty. The results demonstrate that visual affordances (determined by object-hand compatibility) and visual familiarity can directly activate motor responses. Hand differences are discussed in terms of hemispheric specialisation for different components of motor action.

INTRODUCTION

This paper describes the first experimental report of a patient who demonstrates what we will term manual interference effects in behaviour. We examine the conditions that elicit these effects, varying both the stimulus to which action is directed and the goal and nature of the action, and we examine whether these conditions are the same for both hands of the patient. The manual interference in the patient occurred in the context of an "anarchic

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hand syndrome", and we return to discuss the relations between the interference effects we observe experimentally and the patterns of behaviour observed in this syndrome. However, our aim is not to analyse this syndrome as such, but rather to understand how manual interference effects arise and what they can tell us about the processes involved in selecting manual responses to action in the normal brain.

Anarchic and Alien Hand Syndromes

The term "anarchic hand syndrome" was introduced by Della Sala et al. (1991, 1994) to describe behaviours in which involuntary manual actions were made by patients who remained aware that the actions were inappropriate. For example, Goldstein (1908) describes a patient who felt that her left hand had a will of its own that she was unable to control; indeed on one occasion, her left hand grabbed her throat and was choking her, and she had to apply considerable force with her right hand before she was able to pull the left hand away. The term originally used to describe such pathological behaviour was "alien hand syndrome"; however, Della Sala and his colleagues have argued that some clarification of terminology is necessary (Della Sala et al., 1991, 1994). In particular, Della Sala et al. distinguish between pathological manual behaviour of which the patient is *aware*, and which they describe as anarchic hand, and pathological manual behaviour of which the patient is *unaware*, and which they describe as alien hand. In other respects the behaviours exhibited by patients with alien and anarchic hand are similar; descriptions typically include: spontaneous and involuntary grasping by one hand, intervention by one hand to alter the activities of the other, poor voluntary control of the alien hand, and poor bimanual coordination (Della Sala et al., 1991). Alien hand syndrome seems to be associated with posterior lesions of the corpus callosum, and bears similarities to those movements (made outside conscious awareness) that are associated with parietal pathology (i.e. hemisomatognosia, meaning a unilateral loss of knowledge or sense of one's own body and bodily condition). Anarchic hand, on the other hand, is thought to result from anterior lesions of the corpus callosum, lesions of the medial frontal cortex, or both (Brust, 1996).

The term "alien hand" has also been used to describe the involuntary movements shown by patients with corticobasal ganglionic degeneration (CBD) (Doody & Jankovic, 1992; Rinne, Lee, Thompson, & Marsden, 1994). For instance, Gibb, Luther, and Marsden (1989) reported three patients with CBD, all of whom showed abnormality of motor function as their first clinical symptom, with one reported as having alien hand syndrome. Doody and Jankovic (1992) describe five patients with CBD, with apparent alien hand symptoms, and Rinne et al. (1994) reported alien hand symptoms in 14 out of 36 patients with CBD showing motor problems as their primary clinical deficit. The limb affected in these CBC cases is quite heterogeneous, with about equal numbers of patients showing effects with the dominant and the nondominant hand (see Doody &

Jankovic, 1992; Rinne et al., 1994). However, assessments of the patient's awareness of the inappropriate hand movements in such cases is typically not reported, so it is unclear whether the term "alien hand" is appropriate. Also, as noted by Marchetti and Della Sala (1998) "... the pathological hand of these patients is seen to wander involuntarily, and to perform purposeless movements. Often the arm levitates spontaneously, sometimes with tentacular movements of the fingers ...". Such behaviour may be distinguished from the kind of hand movements found in patients with alien and anarchic hand syndromes, which can be stimulus directed. Nevertheless, it is clear that pathological patterns of movement can be demonstrated as important presenting symptoms in CBD. This is relevant to the case we report, who had CBD.

Patients with anarchic hand resulting from frontal lobe and callosal pathology may exhibit "frontal" behaviours such as impulsive and unwilled groping towards objects (utilisation behaviour), and compulsive manipulation of objects with the affected limb; however, such patients may be distinguished from patients with a standard frontal lobe syndrome because they show poor bimanual coordination and signs of intermanual conflict. Signs of callosal disconnection (such as poor tactile naming for objects placed in the left hand, impaired ability to write with the left hand, and left hand apraxia when asked to imitate an examiner's movements or when asked to generate motor actions in response to a verbal command) have been associated with either anterior (Leiguarda, Starkstein, & Berthier, 1989) or posterior (Tanaka, Yoshida, Kawahata, Hashimoto, & Obayashi, 1996) callosal lesions.

Goldberg et al. (1981) were the first to account for what Della Sala et al. term anarchic hand pathology in terms of lesions to the Supplementary Motor Area (SMA) and cingulate cortex. Della Sala et al. (1991, 1994) expanded on this account and proposed that anarchic hand effects arose as a result an imbalance between the neural areas responsible for controlling complex voluntary movements (SMA) and those involved in nonroutine movements under sensory guidance (premotor cortex—PMC). Thus, a dominant anarchic hand would result from damage to the SMA in the left hemisphere, since actions performed by the dominant limb would then be determined by the undamaged left PMC, particularly if any additional callosal lesion had impaired the links between the nondamaged (right) SMA and the left motor cortex (preventing inhibition of the left PMC). As a consequence, the dominant limb would be unable to operate volitionally, and would operate in response to external visual stimuli in an uninhibited way. Della Sala et al. (1994) argue that a pure callosal lesion is unlikely to result in a chronic anarchic hand, although transient anarchic hand may be observed (see Geschwind et al., 1995; Tanaka et al., 1996). Callosal lesions may also cause poor bimanual coordination (see Geschwind et al., 1995). Fine motor movements of the nondominant hand require bilateral activation of motor areas (as shown by functional MRI and PET, Kawashima, Yamada, & Kinomura, 1993; Kim, Ashe, & Hendrich, 1993); a callosal lesion may interrupt the transmission and coordination of information between the premotor areas and motor areas in each hemisphere. The dominant hand is predominantly controlled by the left motor areas and therefore would be unaffected by the callosal lesion.

More recent anatomical studies have shown that SMA consists of two different functional zones: F3 (SMA), and F6 (pre-SMA). In addition, two cingulate motor areas have been identified, so that the medial surface of each hemisphere contains four frontal motor areas in addition to the primary motor cortex (MI) and the PMC (see Freund, 1996). These structures are influenced by inputs from the basal ganglia (in addition to input from posterior cortical structures) (see Alexander & Crutcher, 1990; Alexander, Crutcher, & DeLong, 1990; Alexander, DeLong, & Strick, 1986). Alexander et al. (1986) have described a number of different cortico-striate circuits and have argued that the circuit that involves SMA may be significant in the programming and initiating of internally generated motor programmes. It follows that damage to the SMA circuits, due to subcortical impairment, could also lead to anarchic hand syndrome. The present case, ES, was a patient who in everyday life presented with aspects of anarchic hand syndrome due to CBD. For instance, one hand would sometimes interfere with the actions of the other whilst she was performing a unimanual task. She also reported one occasion on which her left hand jumped involuntarily to hit her aunt whom she was visiting. ES was aware of these interfering responses and that her hands sometimes acted at cross purposes to her intentions in everyday life, suggesting a classification of anarchic hand syndrome. However, we return to discuss the relations between anarchic and alien hand syndromes, and their relevance to the present case, in the General Discussion.

Factors Eliciting Involuntary but Purposeful Hand Activity

In all cases reported to date, the involuntary behaviour has been described clinically, but there have been no attempts to determine the factors that elicit anarchic hand activity. In many cases, the impaired hand is described as acting at cross-purposes to the unaffected hand. For instance, Tanaka et al. (1996, p. 861) noted that "... when asked to place a toothbrush in front of the mirror, he (the patient) took the toothbrush with the right hand ..." but his left hand snatched it from the right hand and put it back where it was ...". However, it is unclear from such an example whether the involuntary activity is activated by some learned association with the visual stimulus (such as the toothbrush should always be placed in this position) or by a separate (right-hemisphere) goal (return objects to their places). By understanding the factors that determine involuntary hand behaviour we may throw important light on how motor actions are selected and controlled in the brain.

In this paper we assess the factors that elicit involuntary upper limb activity in a patient with CBD. By the term manual interference we refer here to instances in which inappropriate responses were made with the one hand when responses are meant to be made with the other hand. ES's problems were apparent in both limbs but did not appear to reflect damage to a common underlying mechanism; rather, different forms of activity were associated with each hand: The right hand behaviour appeared to be responsive to learned associates between visual stimuli and particular actions, and the left to spatial and response uncertainty in the tasks. Importantly, our results suggests that ES's right hand responded on the basis of visual affordances, based on an interaction of the visual properties of an object (including the direction in which it was facing) and the behavioural action required by the task (e.g. point vs. grasp). The data point to the role of visual affordances in selecting actions from objects.

CASE REPORT

ES was a right-handed ex-nursing assistant who was 59 years old at the time of the reported investigations. On neurological examination, her presenting symptom had been increased clumsiness of the right arm and increasing inability to perform activities of daily living such as dressing, managing a knife and fork during eating, writing, etc. Her speech was slightly slurred. On occasion, she would experience sudden jerking movements of the right arm. There had been no history of any precipitating injury and there had been a gradual onset of her symptoms over the previous year. On examination, muscle strength was normal (but she had some action myoclonus), but sensation and proprioception were bilaterally impaired. All the reflexes were brisk, especially in the arm. Her plantar reflex responses were flexor bilaterally. There was a very slight increase of tone on the right. She showed marked drifting in movement of the right outstretched hand. Visual acuity was 6/9 in the left and 6/12 in the right eye. She had a reduced gaze upwards with lateral nystagmus to the right. There were postural and gait disorders (including petit pas). She was reasonably well oriented in time and showed no marked episodic memory deficits in reporting recent events.

The EEG was nonspecific, with an excess of theta and occasional delta waves across both hemispheres.

The radiological report was based on both MRI and CT scans. These showed: (1) Normal cingulate gyri and a fairly normal limbic system. (2) The corpus callosum was normal, although a little thinned posteriorly. (3) The T2 weighted image indicated signal abnormality in the corpus callosum above the lateral ventricles, more on the left than on the right. (4) There was marked atrophy of the sylvian aspect of the left temporal lobe, and of the related insula. (5) There was dilatation of the left temporal horn, and the left trigone (see Fig. 1). Petritrigonal signal abnormality extended into the "u" fibres of the left parieto-occipital cortex, and there was some atrophy of the related gyri. There was also white matter abnormality which could have been due to either small vessel disease or (less likely) to longstanding demyelination. The signal abnormality suggested some changes to the posterior centrum-semiovale and the corpus callosum on the left due to small vessel disease.

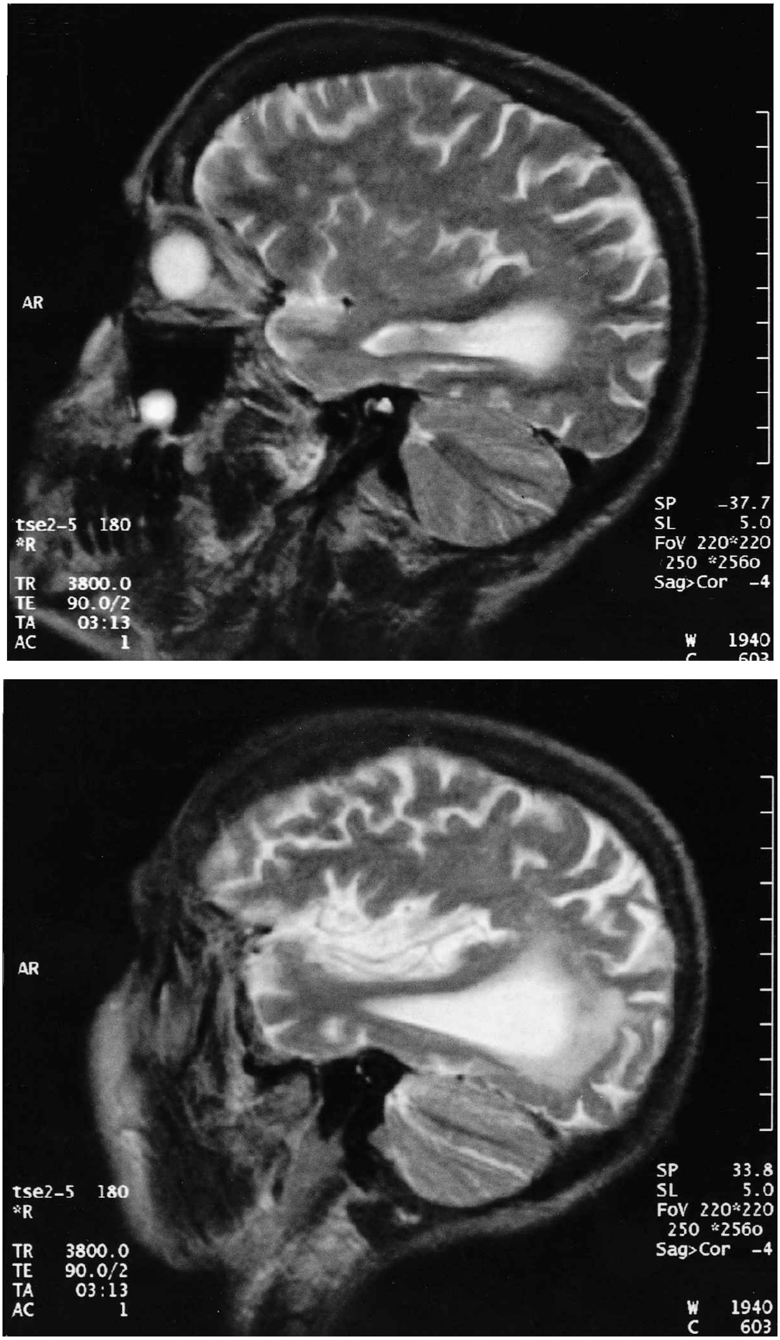


Fig. 1. Sagittal T2-weighted MRI scans (see text for description).

Involuntary Upper Limb Activity

Features of involuntary limb activity were apparent in both the dominant and the nondominant limbs. Thus, a grasp reflex was apparent in the dominant hand. The dominant hand was also noted to drift up in a spontaneous, nonpurposeful way (as has been reported in cases of CBD, Doody & Jankovic, 1992; Rinne et al., 1994). In addition, ES reported that spontaneous, purposeful movements would sometimes occur with her right hand, which interfered with left hand activities. Although she was aware of these movements she was unable to inhibit them. No grasp reflex was observed in the left hand, but this limb was also subject to strong involuntary movements. Intermanual conflict was also a feature of the left hand; on occasion, when ES was asked to perform a task with her right hand, the left hand would grip her right arm and would not let it go.

Neuropsychological Assessments

Detailed neuropsychological assessment focused on visuomotor performance. Testing took place once per week over a 6-month period. During this time there was no obvious deterioration in performance. Tests assessing the functioning of the dorsal visual pathway included the space perception subtests of the VOSP (Visual Object and Space Perception Battery, Warrington & James, 1991), tests for extinction, and tests for simultanagnosia. Tests of the ventral visual pathway included tests of the visual naming of pictures and words, tests of the ability to access the semantic system from vision (using subtests from the Birmingham Object Recognition Battery—BORB; Riddoch & Humphreys, 1993). In addition, we performed further assessments to determine the integrity of ES's semantic system by asking her to provide definitions to auditorily presented words. Tests of motor ability included tests for dyspraxia.

Tests of Space Perception

When assessed using the space perception subtests of the VOSP (Warrington & James, 1991), ES showed a marked impairment (dot counting: 5/10; position discrimination: 9/20; number location: 0/10; cube analysis: 1/10).

Tests of the Ability to Attend Equally to Both Sides of Space

Tests of extinction. Using a Macintosh DuoDock computer, and VScope software (Enns, Ochs, & Rensink, 1990), letters (0.5 × 0.5cm) were presented for identification, 2cm either to the left or the right or both sides of fixation following a central fixation cross. When upper-case letters were exposed for 415msec, ES was able to identify 92% and 89% of single left and right letters respectively, but was only able to identify 26% of simultaneously presented pairs of letters (typically identifying only the left-side letter of the pair). When the exposure duration was doubled (830msec), ES identified 96% of single left, 96% of single right, and 60% of bilaterally presented letters. Similar examples of extinction have been reported in patients with simultanagnosia (Kinsbourne & Warrington, 1962).

Testing for simultanagnosia. ES had a mild simultanagnosia, which was shown in poor performance in interpreting complex pictures of scenes. For instance, ES was unable to describe what was happening in the picture of the "Telegraph Boy" (see Kinsbourne & Warrington, 1962). ES was also mildly impaired in naming pictures of single items (as distinct from scenes). Performance was poorer for more complex pictures with multiple segmentation cues, when she would tend to identify only part of the picture. For example, when asked to identify a picture of a kilt, her response was a "brush" suggesting that she only "saw" the sporran. In general, performance was better in naming animate relative to inanimate items (87% vs. 74% correct for animate vs. inanimate items respectively, where items in both groups had been matched for name frequency). ES's object recognition abilities are presented in detail in Riddoch, Humphreys, and Kapur (in preparation).

Tests of Object Processing

Picture naming. Picture naming was assessed using a subset of items from the Snodgrass and Vanderwart corpus (1980) (76 items in total). Equal numbers of animate and inanimate items were used, items being matched across groups for name frequency (see Humphreys et al., 1988). The pictures were presented in a randomised order one at a time. Responses were not time limited, and, due to ES's dysarthria and anomia, a lenient scoring criterion was applied so that responses that closely approximated the target name were accepted as correct. ES scored 68/76. She showed no effect of name frequency (she scored 34/38 for both high and low name frequency items). She was slightly better at naming items from animate than from inanimate categories (36/38 vs. 32/38 respectively).

Word reading. Some impairment was noted in the reading of single words, as was shown in performance on some of the subtests from the Psycholinguistic Assessments of Language Processing in Aphasia (PALPA; Kay, Lesser, & Coltheart, 1992). There were no significant effects of word length (PALPA test 29, 29/30), word frequency (PALPA test 31, 38/40 and 35/40 for high- and low-frequency words respectively) or imageability (PALPA test 31, 39/40 and 34/40 for high- and low-imageable words respectively). On PALPA test 32 (grammatical class reading), ES scored 100% correct for nouns, adjectives, and verbs, but made 4 errors when reading function words (16/20 correct). No effects of regularity were apparent in her reading (PALPA test 35: 60% and 63.35% correct for regular and exception words respectively). In general, she made visual errors in the reading of single words (e.g. check → chick). Text reading was severely impaired (probably as a result of her simultanagnosia). ES found it impossible to move from one word to the next along a line of text, and to move from one line to the next.

Ability to access the semantic system from pictured stimuli. We used the Association Match Test from the BORB. In this test, the patient has to match an associatively related picture to a target picture. The distractor item is semantically related to the target and its associate. For instance, for the target item "screwdriver", the associate would be a picture of a screw and the distractor picture would be a nail. ES scored 27/30 correct (mean control score = 27.5, SD = 2.4). In an auditory word–picture match test (Kay et al., 1992) ES also performed reasonably well. In this test, five pictures are arranged around a page. One picture corresponds to the target word (e.g. comb). Of the other four, one is a close semantic relation to the target (e.g. brush), one is a more distant semantic relation (e.g. hand mirror), one is visually similar to the target (e.g. caterpillar), and one is unrelated (e.g. spider). ES scored 37/40 (all 3 errors consisted of selecting a close semantic distractor rather than the target item). The mean control score on this test is give as 39.3 (SD 1.07). ES falls just outside 2 SDs of the control score.

Tests of the Ability to Access Stored Knowledge from an Auditory Word. ES was asked to define auditorily presented names which were presented one at a time. The items were the same as those used for the picture naming test. She provided correct definitions for 74 of the 76 items. For two items (one animate and one inanimate item) the definition she produced related partly to the target name and partly to a semanatically related object.

Tests of Motor/Sensory Ability

Tests for dyspraxia. ES showed a bilateral dyspraxia which was independent of the modality of testing. Thirty-six objects were used in each of four conditions (gesture to a visually presented object, gesture to the name of an object, or imitation of a gesture performed by the examiner) for both left and right hands. The data are shown in Fig. 2. Summing across conditions, no significant difference was found between the performance of the left and the right hand [$\chi^2(1) = 2.0$, n.s.]. Summing across hands, performance was shown to differ across the different conditions [$\chi^2(3) = 8.6$, $P < .03$]; this effect was due to poorer performance in the imitation condition [performance across the other three conditions did not differ, $\chi^2(2) = 3.0$, n.s.].

Tests of tactile naming. Bilateral tactile anomia was present (ES correctly named 5/20 objects with the right hand, and 10/20 of the same objects with the left hand).

Writing ability. ES had a marked dysgraphia and was unable to write or copy with either hand.

Signs of callosal disconnection. Signs of callosal disconnection were not clear cut. Signs of relevance in right-handed individuals are: left hand tactile anomia, poor left hand performance on tests of apraxia (particularly gestures to verbal command and imitation of the examiner's hand movements), left hand agraphia, and right hand constructional apraxia.

1. Left hand tactile anomia. ES showed better tactile naming with the left than with the right hand (although both were impaired).

2. Poor left hand performance on tests of apraxia; in particular, gesture to verbal

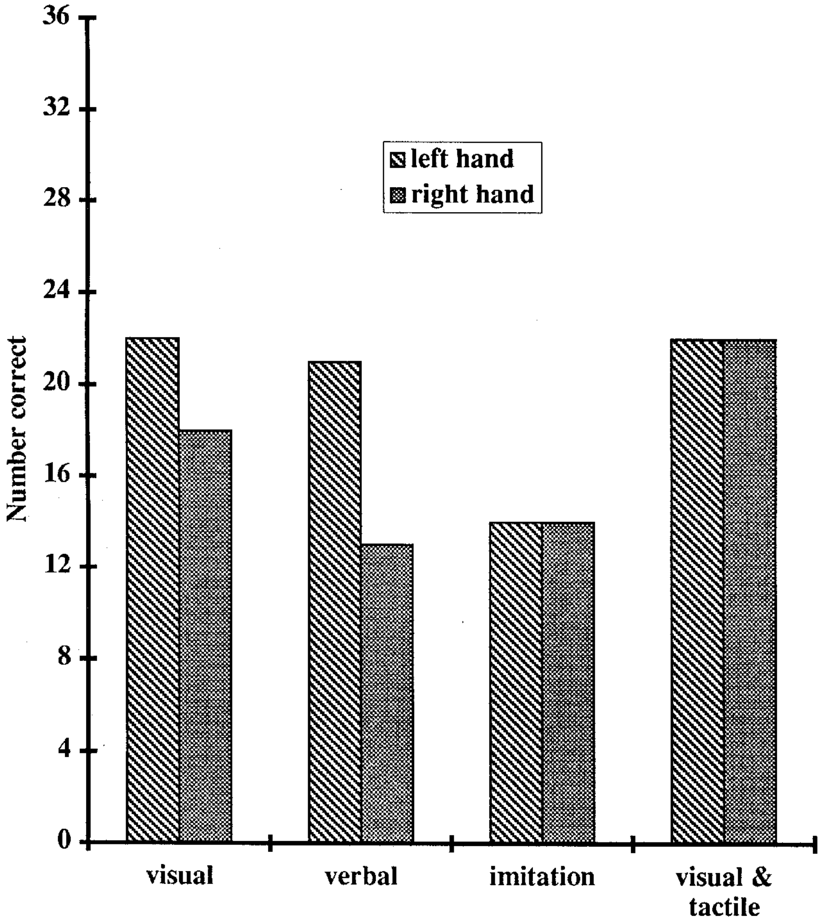


Fig. 2. Gesturing performance according to modality of input.

command and imitation of the examiner's movements. ES performed better to verbal command with the left than the right hand, 23/36 vs. 13/36 correct [this difference was significant, McNemar (1) = 8.1, P = .01]. There was no difference in patterns of performance with left and right hands to imitation (14/36 correct in each case).

3. Left hand agraphia. ES was unable to write or draw with either hand.
4. Right hand constructional apraxia. ES was unable to construct simple designs with either hand.

Spontaneous Speech

Spontaneous speech was dysarthric. Verbal fluency was impaired. ES was only able to generate the names of 8 vegetables, 2 items of fruit, 6 girls and 6 boys names when given 1 minute for each category (scores of below 15 in each category are considered to be impaired; see Lezak, 1983).

Although ES presented with a range of cognitive deficits, the most severe were with visuospatial perception and with motor performance. Recall of recent events was good and she had no clinical deficits in semantic memory. Over the test period there was no evidence of increasing dementia. The deficits in spatial perception and the symptoms of simultanagnosia did not impinge on the tests of manual reaching and grasping that we performed with ES. For all the critical tests stimulus presentation times were unlimited and, as we discuss, ES showed clear evidence of having perceived the stimuli correctly. In addition, her good performance in some conditions showed that she was able to localise stimuli appropriately. During the course of testing we did not observe any florid manifestations of anarchic hand activity; however, one hand would frequently attempt to interfere with a required task. For example, in the assessment of dyspraxia, ES was asked to gesture the use of visually presented objects (either by a pantomime, or by actually using the object). The performance of each hand was assessed separately. It was frequently the case that the left hand would attempt the task when the right hand was the focus of testing and vice versa. The interference was of such a magnitude that ES attempted to sit on one hand while the other was tested for gesturing ability. The interfering effect of one hand on the performance of the other was tested more formally in a series of experimental investigations.

EXPERIMENTAL INVESTIGATIONS

In this section we describe the experimental investigations into the factors that elicit manual interference in ES. We define manual interference as occurring when one limb takes control of a required response in a way that is contrary to the verbal instructions given in the task. In Experiment 1, ES had to point to a light, and the hand for the response was determined by the location of the light; a left hand response was to be made to a light appearing on the left of ES's body, a right hand response was to be made to a light on the right of her body. We examined performance when the light cueing the hand for response was blocked over trials, and when it occurred randomly (so that a response from either hand could occur at random). In the subsequent experiments, responses were again determined by the location of the stimulus, but we varied the nature of the stimulus involved and the required response. The stimulus was a cup or a cup-like object, which could be oriented in various directions (e.g. handle to the left or the right). The response was to point to or pick up the object. We show that manual interference is determined both by the nature of the stimulus (a familiar cup rather than a cup-like object, in a particular orientation) and the required action (picking up rather than pointing).

Experiment 1: Pointing to Lights

This experiment consisted of five separate conditions. The methodology for each condition was similar. The first three conditions were blocked (e.g. Condition 1: bilateral lights; Condition 2: unilateral left-side lights; Condition 3: unilateral right-side lights) and in the final two conditions lights were presented randomly to the left or right or both sides of space (Condition 4: lights occurring on left or right sides of space; Condition 5: lights occurring on left or right or both sides of space). The blocked conditions were run before the random conditions. ES was asked to point to the light (or lights) that had brightened, the hand for the response being determined by the location of the light; a left hand response was to be made to a light appearing on the left of ES's body, whereas a right hand response was to be made to a light on the right of her body.

Method

On each trial, ES was required to place her index fingers on two starting positions placed in front of her (one on either side of midline). She faced two light-emitting diodes (LEDs) placed 40cms away from her. Each LED was located 20cms from the midline. When a LED (or LEDs) lit, she was asked to place the index finger onto the LED (left index finger for a left-side LED, right index finger for a right-side LED). ES was asked to perform accurately and told that there were no time limits on responding. She was given the specific instruction for each condition prior to each trial block, and she was reminded of the instruction at intervals throughout. No feedback was given during a trial block. Performance was recorded using a video camera.

Results

The results are given in Table 1. In Condition 1 (bilateral blocked presentation) ES never initiated movements to both left and right LEDs simultaneously (although she had been asked to do so). She would first touch the left-sided LED with her left hand before touching the right-side LED with her right hand. On three trials she failed to use the right hand at all, instead touching both left-side and right-side LEDs with her left hand (going first to the left LED). On one trial she failed to use her left hand, touching both left- and right-side LEDs with her right hand (going first to the right LED).

In Condition 3, ES made one error (using her left hand to point to the right-side LED). The error was made on the first trial of the block after she had just completed Condition 2.

Table 1. Results of Experiment 1

Condition	*Total No. of Trials per Condition*	*Per Cent Correct*
Condition 1: Bilateral blocked presentations	32	87.5
Condition 2: Unilateral blocked left presentations	24	100.0
Condition 3: Unilateral blocked right presentations	24	95.8
Condition 4: Random unilateral left or right presentations	64	96.9 left[a] 56.3 right[b]
Condition 5: Random bilateral and unilateral left and right presentations	71	95.8 left[a] 58.3 right[b] 60.9 bilateral[c]

[a]Left-side LEDS.
[b]Right-side LEDs.
[c]Bilateral LEDs.

In Condition 4 (random unilateral left or right presentations) ES scored particularly poorly when responding to the right-side light (18/32 correct). On 14 occasions she reached for the right light with her left hand. In this condition, left hand responses were significantly better than right hand responses ($\chi^2(1) = 14.7$, $P < .0001$].

In Condition 5 (random bilateral and unilateral left and right presentations) ES again performed poorly when responding to right-side LEDs (14/24) correct. On 10 occasions she reached for the right-side LED with the left hand. When lights appeared randomly either on the left- or on the right-side, ES performed significantly better on left- than on right-side responses [$\chi^2(1) = 9.6$, $P < .002$]. With bilateral presentations, ES scored 14/23 correct (on 9 occasions she touched both left and right LEDs with the left index finger, going first to the left-side LED). Performance in the bilateral trials condition differed significantly from that in the unilateral left condition [$\chi^2(1) = 8.6$, $P < .003$], but not from that in the unilateral right condition [$\chi^2(1) = 0.03$, n.s.].

Error Analysis

A total of 40 errors were made in Experiment 1, representing 16% of all trials. Of these errors, 93% (37) were caused by the left hand going to the incorrect location; and 7% (3) were due to the right hand going to the incorrect location.

Discussion

ES performed relatively well when the light positions and the required motor responses were blocked; however, when the task conditions changed and when both the positions of the LED and the hand for response had to change at random across trials she began to make errors (but only to the right-side and not to the left-side LED). The data demonstrate that ES manifested manual interference behaviour with her left hand, but that this behaviour was elicited under certain circumstances: Either when there was locational uncertainty, or when there was a response uncertainty, or both (with stimuli appearing randomly on left or right). For instance, it may be that ES was able to inhibit her involuntary left hand responses when only the right hand had to be used across a block of trials. Alternatively, when the right target was predictable, ES may have preprogrammed a right hand movement to it, giving dominance to this response; when the target's location was unpredictable, the right hand response may not have been preprogrammed and instead the left hand response was directly invoked by the stimulus. The present results are not simply due to the order of presentation of the conditions in the test session and have been replicated with the orders reversed. Experiment 2 sought to tease apart whether locational uncertainty or response uncertainty was crucial for ES's manual interference. First we assessed her performance when the stimulus location was predictable but the hand of response varied. Second, we assessed performance when the hand of response was predictable but the location of the stimulus varied.

Experiment 2a: Pointing to a Constant Location

This experiment consisted of three separate conditions. In response to a centrally-located written cue (either "Left" or "Right"), ES was required to point with the appropriate hand to the position of the cue. The first two conditions were blocked (e.g. "Left" cue for Condition 1 and "Right" cue for Condition 2). In the third condition the written cue varied randomly from "Left" to "Right" (there being equal numbers of left and right trials in total). The experiment was then repeated but the ordering of the first and second conditions was reversed. The hand for the response was determined by the nature of the cue; a left hand response was to be made to the word "Left", a right hand response was to be made to the word "Right".

Method

At the start of each trial, ES was required to place each index finger on two starting positions placed in front of her (one on either side of midline). She faced a VDU placed 40cms away from her and sunk into the table top (so that it faced upwards). SuperLab software was used to set up the experiment. Each trial was initiated by a keypress, which triggered the removal of a white, central fixation cross on a blank screen with a blank for 1000msec followed by a centrally positioned target word (either "Left" or "Right" written in Times font, size 36, in white). The word was presented for 5000msec, its offset triggered another blank for 3000msec, followed by the fixation cross once more. ES was asked to reach forward with the appropriate hand (left in response to the word "Left", right in response to the word "Right") as soon as the word appeared on the VDU. Once ES had touched the VDU screen, the experimenter initiated the next trial. There were 20 trials in Condition 1 and 2, and 40 in Condition 3 (the words "Left" and "Right" appeared randomly, but with equal numbers of trials for each). On the first run through of the experiment, Condition 1 preceded Condition 2, which preceded Condition 3. On the second run through, the ordering of Conditions 1 and 2 was reversed. On the second run through there was a total of 22 trials in Condition 3.

Results

Performance for the different presentations of the same condition did not differ and the data were amalgamated. The results are presented in Table 2. There was no significant difference in performance in Condition 1 and 2 [$\chi^2(1) = 0.39$, $P < .05$]; nor was there any difference in performance between Condition 1 and the responses to the "Left" cue in Condition 3 [$\chi^2(1) = 1.26$, $P < .05$]. Performance in response to the "Left" cue and the "Right" cue in Condition 3

Table 2. Results of Experiment 2a

Condition	*Total No. of Trials per Condition*	*Per Cent Correct*
1. Cue word: "Left"	40	87.5
2. Cue word: "Right"	40	82.5
3. Random presentation of cue words: "Left" and "Right"	66	77.4 left[a] 35.5 right[b]

[a]Left hand to "Left" cue.
[b]Right hand to "Right" cue.

differed significantly [$\chi^2(1) = 11.09$, $P < .0007$], as did performance in Condition 2 and responses to the "Right" cue in Condition 3 [$\chi^2(1) = 16.38$, $P < .0001$]. Performance with the "Right" cue in Condition 3 (random presentations) was worse than in any other condition.

Error Analysis

A total of 39 errors were made in Experiment 2a, representing 14.7% of all trials. In Conditions 1 and 2, errors always consisted of a response by the incorrect hand. In Condition 3, 19 errors (70.4%) were also of this form; however, 8 errors (29.6%) consisted of no movement being made at all. ES said that she felt unable to move on these occasions. Of the total errors, 8 (20.5%) were caused by incorrect right hand responding, and 23 (59.0%) by incorrect left hand responding.

Experiment 2b: Pointing with a Constant Hand

Experiment 2b consisted of three separate conditions. The first two conditions were blocked. In Condition 1, ES was asked to point to LEDs, which lit randomly in left and right locations, with the left hand. Condition 2 was the same as Condition 1 but ES was asked to respond with the right hand. In Condition 3 the LEDs lit randomly in left and right locations, as before, but now ES was asked to respond to a left-side LED with the left hand and a right-side LED with the right hand.

Method

As in Experiment 1, ES was required on each trial to place her index finger on two starting positions placed in front of her (one on either side of midline). She faced two LEDs placed 40cms away in depth. Each LED was located 20cms from the midline. When an LED (or LEDs) lit, she was asked to place an index finger onto the LED. In two blocked conditions, ES was to respond consistently with the same hand (the left hand in Condition 1, the right hand in Condition 2). In Condition 3, a mixed condition, she was asked to respond to a left-side light with the left hand, and a right-side light with the right hand. Left and right LEDs lit randomly. ES was asked to perform accurately and told that there were no time limits on responding. She was given the specific instruction for each condition prior to each trial block, and she was reminded of the instruction at intervals throughout. No feedback was given during a trial block. Performance was recorded using a video camera. She performed half the blocked location trials first, followed by the random location trials, followed by the remaining blocked location trials.

Results

The results are displayed in Table 3. Performance in the two blocked conditions was not consistent; ES performed significantly better in Condition 1 with her left hand than in Condition 2 with her right hand [$\chi^2(1) = 11.6$, $P < .0007$]. In the mixed condition (Condition 3), she also performed better with her left than with her right hand [$\chi^2(1) = 8.5$, $P < .004$]. There was no significant difference between performance with the right hand in Condition 2 and Condition 3 [$\chi^2(1) = 0.5$, $P < .05$].

Table 3. Results of Experiment 2b

Condition	No. of Trials	Per Cent Correct
1. Left hand to both left and right LEDs	20	100
2. Right hand to both left and right LEDs	20	55
3. Left hand to left LED, right hand to right LED	20[a]	100 left[b] 65 right[c]

[a]Trials for each location.
[b]Left hand to left LED.
[c]Right hand to right LED.

Error Analysis

A total of 16 errors were made in Experiment 2b, representing 20% of all trials. No errors were made in Condition 1; in Conditions 2 and 3 the errors consisted of left hand responses when ES should have been responding with her right hand.

Discussion

In Experiments 2a and 2b we sought to determine whether response uncertainty (Experiment 2a) or locational uncertainty (Experiment 2b) was the significant factor in eliciting manual interference with ES. The results showed that both of these factors are significant; but interestingly, similar results did not obtain in the two experiments. In Experiment 2b, as in Experiment 1, the predominant error type was left manual interference (i.e. the left hand responding when a right hand response was required). In Experiment 2a, some right hand errors occurred (ES made a right hand instead of a left hand reaching response). These data suggest that under conditions of *response* uncertainty, both left and right hands may be preprogrammed to initiate the action and sometimes responses are invoked by the wrong signal. However, in conditions of *locational* uncertainty, left manual interference responses dominate. The data suggests that ES finds it difficult to inhibit hand responses when the processes that initiate the actions are activated under conditions of response uncertainty. Furthermore, processes in the right hemisphere may dominate coding of the spatial parameters of actions under conditions of locational uncertainty, with the result that left manual interference responses are most prevalent under those conditions. In the subsequent experiments we explore more closely how the nature of the required response affects ES's performance. In Experiments 1 and 2 the conditions requiring a response were somewhat artificial (pointing to the location of a target light); in Experiment 3 we explored whether a familiar action (that of grasping and picking up a cup) would also elicit manual interference.

Experiment 3: Picking Up Cups

In Experiment 3 we changed the motor task from pointing to grasping and picking up. Pointing is not a response associated with a particular stimulus; in contrast, actions such as grasping and picking up are, since there are some stimuli to which this response is specifically associated (e.g. a cup). In addition, pointing and grasping may be mediated by different brain areas (see Jeannerod, 1997). It is possible that manual interference responses reflect overlearned (inhibited) associations between visual stimuli and hand responses. Consequently such responses may be invoked by the presence of an eliciting stimulus (e.g. a cup) in the context of a required response (grasping and picking up). If this proposal is correct, we might expect manual interference behaviour to be particularly pronounced in tasks requiring the grasping and picking up of familiar objects.

The targets for the grasping and picking up actions in Experiment 3 were cups. As in Experiment 1, the target could appear on the left or right of ES, and the required response was determined by the target's position. However, in addition to this general manipulation of the target's position, we also varied the position of the handle, which could be on the left or the right of the cup. An overlearned response may be evoked not only by the general class of stimulus (the cup) but the location of its parts relative to an effector. For instance, a right hand response may be evoked when the handle is on the right of the cup, and a left hand response when it is on the left. A manual interference response would take place when the left hand is used to pick up the cup on ES's right, or when the right hand is used to pick up a cup on her left. Here we test whether such responses occur particularly when the cup on the right has its handle on the left (evoking a left hand response) or when the cup on the left has its handle on the right (evoking a right hand response). Note that effects that are specific to the position of the handle of the cup would show that ES's performance is not just due to poor localisation of the cup. Also, her localisation of left-side stimuli in Experiments 1 and 2 (indicated by her left hand responses) were good.

There were 8 experimental conditions, 4 requiring unimanual and 4 requiring bimanual responses. The experiment was repeated 3 times (there was a gap of 1 week between test sessions), giving a total of 30 trials per condition.

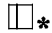
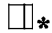
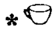
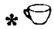
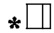
Method

As in Experiment 1, ES was asked to place both index fingers on starting positions in front of her. Either a single cup was placed on the left or the right, or two cups were placed on left and right locations (the distance from the location markers to the edge of the table was 30cm, the distance between the markers was 40cm, each equidistant from ES). There were eight conditions, four requiring unimanual responses and four requiring bimanual responses: ES was asked to pick up left-side cups with the left hand and right-side cups with the right hand by the handle *regardless* of whether the handle was positioned on the left or the right side of the cup. ES was asked to perform accurately and told that there was no time limits on responding. The conditions were presented randomly. No feedback was given, and the instructions were repeated at frequent intervals. Performance was recorded using a video camera.

Results

Unimanual conditions. Basic data for the unimanual conditions are presented in Table 4. The cross indicates the position of the cup relative to midline. ES performed well in the

Table 4. Experiments 3-6: Percentage Correct Responses in Each of the Conditions with Unilateral Presentations

	Experiments							
	3: Pick Up Cup by Handle		*4: Point to Cup Handle*		*5: Pick Up Cup-like Nonobject*		*6: Pick Up Upside-down Cup by Handle*	
Condition	*(N = 30)*[a]		*(N = 20)*[a]		*(N = 20)*[a]		*(N = 20)*[a]	
1		97		100		95		100
2		13		90		0		25
3		7		10		0		0
4		100		95		95		65

[a]*N*= number of trials per condition.

two unimanual conditions where the position of the cup handle was congruent with the side of the responding hand (Condition 1 and 4). There was no significant differences in the scores in these two conditions (Fisher Exact Probability, $P = .05$). ES performed poorly in the two condition where the position of the handle was not congruent with the side of the responding hand (Conditions 2 and 3). Again, there was no significant difference in the scores in these two conditions (Fisher Exact Probability, $P = .4$), but the nature of the error differed in the two conditions. Thus, in Condition 2 and 3, despite instructions, ES would invariably pick up the cup with the right and left hands respectively. Condition 1 was performed significantly better than Conditions 2 and 3 [$\chi^2(1) = 42.1$, $P < .0001$, and 48.7, $P < .0001$ for Conditions 2 and 3 respectively]. Condition 4 was also performed significantly better than Conditions 2 and 3 [$\chi^2(1) = 45.9$, $P < .0001$, and 52.5, $P < .0001$ for Conditions 2 and 3 respectively]. The numbers of the different error types are shown in Table 5.

Bimanual conditions. The results are presented in Table 6. Performance in the bimanual conditions was generally poor apart from Condition 7 (where, like Conditions 1 and 4, the positions of the cup handles were congruent with the side of the responding hands). Condition 7 was performed significantly better than conditions 5, 6, and 8 [$\chi^2(1) = 32.3$, $P < .0001$, 33.6, $P < .0001$, and 52.3, $P < .0001$ for Conditions 5, 6, and 8 respectively]. There was no significant difference in performance in Conditions 5, 6, and 9 [$\chi^2(1) = 5.2$, $P < .07$]. The nature of the errors differed across the different conditions. In Condition 5, ES would typically pick up first the left-side and then the right-side cup with the left hand. For subsequent analyses, these responses were classed as left hand interference errors. On two occasions she picked up the left-side cup with the right hand and the right-side cup with the left hand—a "crossed hand" error. A mirror-image pattern of errors were shown in Condition 6; ES would first pick up the right-side cup and then the left-side cup both with the right hand. There were two main error types in Condition 8. Crossed hand re-

Table 5. Interference Responses to Handles as a Function of the Conditions with Unimanual and Bimanual Presentations: Experiment 3 (Pick Up Cups)

a: Unimanual Trials: Total Errors 55/120

	Condition			
Hand	1	2	3	4
Left hand			28	
Right hand	1	26		

b: Bimanual Trials: Total Errors 77/120

	Condition			
Hand	5	6	7	8
Left hand to both cups	22			12
Right hand to both cups		23		2
Mixed (left hand to right cup, right hand to left cup)	2		1	15

sponses accounted for 52% of the total errors; 41% involved her using the left hand to pick up both the left- and the right-side cups. On two occasions she picked up both cups with the right hand. The numbers of different types are presented in Table 5.

Error Analysis

Summing over unimanual and bimanual conditions, a total of 132 errors were made in Experiment 3 (representing 55% of all trials). Of the total, 47% (62) were caused by the left hand picking up the right cup, or the right cup as well as the left cup; while 39% (52) were caused by the right hand picking up the left cup, or the left cup as well as the right cup. The pattern of errors therefore differs markedly from the pattern shown in Experiment 1. In Experiment 1 errors were rarely made with the right hand. Note that the good left hand performance in pointing to left-side stimuli in Experiment 1 demonstrates that right manual interference here was not due simply to poor location discrimination.

Table 6. Experiments 3-6: Percentage Correct Responses in Each of the Conditions with Bimanual Presentations

	Experiments			
	3: Pick Up Cup by Handle	*4: Point to Cup Handle*	*5: Pick Up Cup-like Nonobject*	*6; Pick Up Upside-down Cup by Handle*
Condition	*(N = 30)*[a]	*(N = 20)*[a]	*(N = 20)*[a]	*(N = 20)*[a]
5	20	50	55	5
6	23	100	90	20
7	97	95	100	90
8	3	35	50[b]	0

[a] *N*= number of trials per condition.

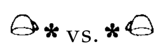
[b] There were only 18 trials in Condition 8, Experiment 5.

Discussion

ES performed well in those conditions where the position of the handle and the position of the cup were congruent with the required response (unimanual Conditions 1 and 4 and bimanual Condition 7). However, when the position of the handle was congruent with the opposite effector (unimanual Conditions 2 and 3, and bimanual Conditions 5, 6, and 8), ES made a large number of errors. In particular, she responded (incorrectly) by grasping and picking up using the hand associated with the position of the handle on the cup. As in Experiments 1 and 2, when incorrect hand responses occurred, ES was typically unaware of them and thought that she had responded correctly. Now, however, the manual interference responses occurred with both hands and were not confined to left hand responses into her right field. The data demonstrate that manual interference behaviour can reflect overlearned and uninhibited responses to stimuli, since in this case a right hand manual interference response was evoked by a learned left-field stimulus. Moreover, the response was determined by the locations of the parts relative to the whole stimulus (left- vs. right-side handles) and not just the spatial location of the cup itself. As we outline in the General Discussion, this result has important implications for understanding how motor responses are evoked and selected in the brain.

In Experiments 4 to 6 we tested whether the pronounced manual interference responses shown with both hands in Experiment 3 were due to the presence of the familiar stimulus (the cup), the fact that a grasping response was activated, or both. In Experiment 4, ES was again presented with cups but on this occasion she was asked to make a pointing rather than a grasp response. This assessed whether the presence of the cup alone was sufficient to elicit bilateral manual interference behaviour. In Experiment 5, ES again made grasp responses but this time was presented with nonobjects that were cup-like in shape. This assessed whether activation of the grasp response was sufficient to generate pronounced manual interference responses by each hand. In Experiment 6, ES made grasp responses but this time to inverted cups. This last study tests whether the familiar stimulus need to be in the correct orientation for manual interference behaviour to be evoked. Note that, with an inverted cup, the handle can be on the left or right of the cup (although now the positioning is towards the bottom rather than the top of the stimulus, so performance should be similar to that in Experiment 3 if the location of the handle alone was important). In addition, Experiment 6 tests for one other possible account for the results in Experiment 3. That is, that ES made manual interference responses to cups when their handles were incongruent with their locations; for instance:

possibly because ipsilateral grasp responses are relatively difficult to execute. If this were the case, performance should remain the same in Experiment 6, when the cups were inverted.



Experiment 4: Pointing to a Cup Handle

Method

As in the previous experiments, ES was asked to place both index fingers on starting positions in front of her. Either a single cup was placed on the left or the right, or two cups were placed on left and right locations (the locations were identical to those in Experiment 3). There were eight conditions, four requiring unimanual responses and four requiring bimanual responses ES was asked to *point* to left-side cups with the left hand and *point* to right-side cups with the right hand regardless of whether the handle was positioned on the left or the right side of the cup. ES was asked to perform accurately and told that there were no time limits on responding. No feedback was given, and the instructions were repeated at frequent intervals. Performance was recorded using a video camera. There were equal numbers of trials (20) in each condition, and conditions were randomised over trials.

Results

Unimanual conditions. Accuracy data for the unimanual conditions are presented in Table 4. The cross indicates the position of the cup relative to midline. As in Experiment 3, ES performed well in the two unimanual conditions where the position of the cup handle was congruent with the side of the responding hand (Conditions 1 and 4). There was no significant difference in the scores in these two conditions (Fisher Exact Probability, $P > 1.0$). Unlike Experiment 3, ES performed poorly in only one of the two conditions where the position of the handle was not congruent with the side of the responding hand, thus performance was poor in Condition 3 but was relatively good in Condition 2 [this difference was significant, $\chi^2(1) = 25.6$, $P < .0001$]. Significantly fewer errors were made in Condition 2 in Experiment 4 relative to the same condition in Experiment 3 [$\chi^2(1) = 31.9$, $P < .0001$]. There was no significant difference in the patterns of performance shown in Condition 3 in Experiment 3 and 4 (Fisher Exact Probability, $P > 1.0$). ES made a total of 21 errors in the unimanual conditions. Of these, 90.5% (17) consisted of the left hand pointing to the right-side cup (the majority of these errors, were made in Condition 3, and 1 such error was made in Condition 4). Only 9.5% (2) errors consisted of the right hand pointing to the left-side cup (these errors were made in Condition 2 when the handle of the cup was located on the right of the cup). Error data are shown in Table 7.

Bimanual conditions. The accuracy results are presented in Table 6. As in Experiment 3, performance was good in Condition 7, where the positions of the cup handles were congruent with the side of the responding hands. Unlike Experiment 3, performance was also good in Condition 6. There was no significant difference in performance between Conditions 6 and 7 in Experiment 3 (Fisher Exact Probability, $P > 1.0$), but there was a significant difference between performance in Condition 6 in Experiments 3 and 4 [$\chi^2(1) = 28.4$, $P < .0001$]. ES did not respond to the left-side cup with her right hand in Experiment 4 as she had done in Experiment 3. In general, performance was better

Table 7. Interference Responses to Handles as a Function of the Conditions with Unimanual and Bimanual Presentations: Experiment 4 (Point to Cup Handle)

a: Unimanual Trials: Total Errors 21/80

	Condition			
Hand	*1*	*2*	*3*	*4*
Left hand			18	1
Right hand		2		

b: Bimanual Trials: Total Errors 24/80

	Condition			
Hand	*5*	*6*	*7*	*8*
Left hand to both cups	10			10
Right hand to both cups			1	1
Mixed (left hand to right cup, right hand to left cup)				2

in the bimanual conditions in Experiment 4 relative to Experiment 3 [i.e. fewer errors were made in Conditions 5 and 8, $\chi^2(1) = 5.0$, $P < .03$, and $\chi^2(1) = 9.0$, $P < .003$, respectively]. Error types are presented in Table 7.

Error Analysis

Overall, a total of 45 errors were made in Experiment 4 (representing 28% of all trials). Significantly fewer errors were made in Experiment 4 relative to Experiment 3 [$\chi^2(1) = 28.1$, $P < .0001$]. The *nature* of the errors also differed across Experiment 3 and 4. The majority of errors resulted from left-hand pointing (either to a single right-side cup or to both left and right-side cups) (87% or all errors, $N = 39$). The converse error (right hand pointing) occurred relatively infrequently (9% of all errors, $N = 4$) as compared to 39% of total errors in Experiment 3. Two errors were of the "crossed" type (i.e. left hand to right location, right hand to left location).

Discussion

The nature of the required response differed in Experiments 3 and 4 (point rather than pick up). This had the effect of reducing the overall errors in Experiment 4; interestingly, right hand activity was also rarely apparent (as it had been in Experiment 3). For left-side stimuli, performance resembled that in Experiment 1, in that ES rarely made right hand responses to the left side. This suggests that these responses are modulated by activation of the required response (grasping, as in Experiment 3, relative to pointing, as here). For right-side stimuli, however, a different pattern of performance emerged. Now performance was affected by the orientation of the cup (or its handle). Left manual interference responses were more likely when the cup (or the handle) was in a familiar orientation. For the left hand, then, the response associated to the stimulus (the grasp response) did not need to be activated for manual interference to occur. This confirms our findings from Experiment 1, where manual interference responses occurred when ES made left hand pointing actions to right-side stimuli. However, the data also show that the mere presence of a right-side stimulus was not sufficient, and that left hand responses were modulated by the orientation of the stimulus. Left hand responses did not occur here with right-oriented cups, for example:

* 

Thus the left hand, like the right hand, was affected by the stimulus, but the left hand was less affected by the response (errors occurring when ES had to grasp *and* when she had to point). Note that, since stimulus orientation affected left hand performance, it is unlikely that ES's left manual interference simply reflected misjudgement of the spatial location of right-side stimuli.

Experiment 5: Picking Up Nonobjects

Method

As in the previous experiments, ES was asked to place both index fingers on starting positions in front of her. Either a single nonobject was placed on the left or the right, or two nonobjects were placed on left and right locations (the locations were identical to those in Experiments 3 and 4). The nonobjects were constructed to be cup-like in that there was a side-positioned handle. The blocks were 6cm × 6cm × 10cm with a smaller block 2cm × 2cm × 10cm, positioned centrally on one of the long sides. As in Experiments 3 and 4, there were eight conditions, four requiring unimanual responses and four requiring bimanual responses. ES was asked to pick up left-side nonobjects with the left hand and right-side nonobjects with the right hand regardless of whether the "handle" was positioned on the left or the right side of the nonobject. ES was asked to perform accurately and told that there were no time limits on responding. No feedback was given, and the instructions were repeated at frequent intervals. Performance was recorded using a video camera. There were equal numbers of trials (20) in each condition (except for Condition 8 where there were only 18 trials), and conditions were randomised over trials.

Results

Unimanual conditions. Accuracy data for the unimanual conditions are presented in Table 5. The cross indicates the position of the nonobject relative to midline. As in Experiment 3, ES performed well in the two unimanual conditions where the position of the cup handle was congruent with the side of the responding hand (Conditions 1 and 4). ES performed poorly in the two conditions where the position of the handle was not congruent with the side of the responding hand (Conditions 2 and 3). However, Experiments 3 and 5 differed in the nature of the errors performed. For instance, performance in Condition 2 was poor, and did not differ from that in the same condition in Experiment 3 (Fisher Exact Probability, $P = .99$, n.s.). However, while ES used her right (incorrect) hand to pick up the cup in Experiment 3, this error type was performed only twice in Experiment 5. The majority of errors (18) consisted of ES grasping the blocks from above, rather than from the side using the "handle" ("grasp errors"). Since she had been instructed (and was frequently reminded) that she should perform the pick-up by the handle, picking up from the top was classified as an error even though the correct (left) hand was used. Performance was poor in Condition 3 as it had been for the same condition in Experiment 3 (there was no significant difference in numbers of correct trials in this condition in the two experiments, Fisher Exact Probability, P = .51, n.s.). However, whereas in Experiment 3 ES typically picked up the cup using her left hand, the same error occurred on only 50% of the error trials here. The other errors consisted of picking the blocks up from above (with the right hand on 9 occasions and with the left hand on 1 occasion). Error responses to handles are presented in Table 8. "Grasp errors" are given in Table 9.

Table 8. Interference Responses to Handles as a Function of the Conditions with Unimanual and Bimanual Presentations: Experiment 5 (Pick Up Cup-like Non Objects)

a: Unimanual Trials: Total Handle Errors 12/80

	Condition			
Hand	*1* □*	*2* □*	*3* *□	*4* *□
Left hand			10	
Right hand		2		

b: Bimanual Trials: Total Errors 15/78

	Condition			
Hand	*5* □*□	*6* □*□	*7* □*□	*8* □*□
Left hand to both cups	8			5
Right hand to both cups				2
Mixed (left hand to right cup, right hand to left cup)				

Bimanual conditions. The results are shown in Table 6. The cross indicates the position of the nonobject relative to midline. In general, performance was better in the bimanual conditions in Experiment 5 than it had been in Experiment 3. In Condition 5, ES made a number of errors but performance was better than that in the same condition in Experiment 3 [$\chi^2(1) = 8.1$, $P < .004$]. ES used her left hand to pick up both left and right blocks on eight occasions (the pick-up was always correct, i.e., by the "handle"). On one occasion ES picked up the right-side block with the correct (right) hand but from above rather than by the "handle". In Condition 6, performance was good and was significantly different from performance in the same condition in Experiment 3 [$\chi^2(1) = 21.3$, $P < .0001$]. On two occasions ES picked both sets of blocks up (consecutively) with the left hand; the correct grip was used for the left-side blocks, but she picked up the right-side blocks from above with fingers griping the small block. These were classed as "grasp errors". Performance in Condition 7 was good and did not differ significantly from the same condition in Experiment 3 [$\chi^2(1) = 3.7$, $P >$

Table 9. Grasp Responses to Cup-like Nonobjects as a Function of the Conditions with Unimanual and Bimanual Presentations: Experiment 5 (Pick Up Cup-like Non Objects)

a: Unimanual Trials: Total Grasp Errors 30/80 (28 with the Correct Hand, 2 with the Incorrect Hand)

	Condition			
Hand	*1* □*	*2* □*	*3* *□	*4* *□
Left hand	1	18	1	1
Right hand			9	

b: Bimanual Trials: Total Errors 4/78 (All with the Incorrect Hand)

	Condition			
Hand	*5* □*□	*6* □*□	*7* □*□	*8* □*□
Left hand to both objects		2		
Right hand to both objects	1			1
Mixed (left hand to right object, right hand to left object)				

.054]. Performance in Condition 8 was better than in the same condition in Experiment 3 [$\chi^2(1) = 14.9, P < .0001$]. Most errors were of the left hand picking up both left and right blocks (5/9; in all instances the correct grip was used); on two occasions the converse error was performed with the right hand picking up both sets of blocks. On one occasion the left-side block was neglected, and on occasion ES picked up the right-side blocks with the correct hand but grasped the big rather than the little block from the side. Interference responses to handles are given in Table 8. "Grasp errors" are presented in Table 9.

Error Analysis

Overall, a total of 62 errors were made in Experiment 5 (representing 38.8% of all trials); fewer errors were made in Experiment 5 than in Experiment 3 [$\chi^2(1) = 10.1, P < .001$]. The nature of the errors also differed between Experiment 5 and 3 (see Table 10) in that "grasp errors" emerged in Experiment 5. The task required that the blocks were picked up by the "handle". However, ES frequently failed to perform the task in this way, and tended to pick up the blocks from the top rather than by the "handle"; 54.8% (34) of all errors were of this "grasp" form (of these, 67.6% [23] and 32.4%[11] were made by the left and right hands respectively). Interestingly, grasp errors were predominantly made with the correct hand for the side, unlike the manual interference responses to the handle. Only 6/34 grasp errors were with the wrong hand, and 28/34 were with the correct hand (see Table 10). All incorrect responses to the handle were made with the wrong hand.

If responses are scored simply in terms of the hand used (the nature of the grasp being disregarded), the differences between Experiment 3 and 5 become apparent in that there are a greater proportion of left hand to right hand errors in Experiment 5 (see Table 10).

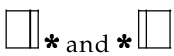
Table 10. Differences in Errors between Experiments 3 and 5

Grasp	*Errors*	*Expt. 3*	*Expt. 5*
Correct grasp (by handle); incorrect target	% with the left hand	47.0	37.0
	% with the right hand	39.0	6.5
Incorrect grasp (by top of object); incorrect target	% with the left hand	0.0	37.0
	% with the right hand	0.0	17.8

Discussion

The overall pattern of correct performance was similar to Experiment 3. Performance was very good when the position of the handle was congruent with the hand of response:

and it was poor when the hand and the effector were incongruent



However, unlike Experiment 3, manual interference responses were not predominant in the incongruent conditions. With a left-side, incongruent stimulus, the majority of errors involved the left hand grasping the blocks from above rather than the side. With a right-side, incongruent stimulus, ES made an equal number of top-grasp responses with her right hand and manual interference grasps with her left hand. Hence manual interference behaviour was modulated by the familiarity of the stimulus. For both hands such behaviour was more likely to be invoked by a familiar cup (in Experiment 3) than by an unfamiliar cup-like nonobject (Experiment 5; although, as in Experiment 4, the manipulation affected right hand responses more than left hand responses). In Experiment 6 we tested the effects of stimulus familiarity further by having ES make grasping responses to inverted cups.

Experiment 6: Picking Up Upside-down Cups

Experiment 6 was identical to Experiment 3 except that ES was asked to pick up cups that had been inverted onto the table top.

Method

As in Experiment 1, ES was asked to place both index fingers on starting positions in front of her. Either a single cup was placed on the left or the right, or two cups were placed on left and right locations (the distance from ES to the location markers was 30cm, and each location was positioned 20cm from the midline). There were eight conditions, four requiring unimanual responses and four requiring bimanual responses. There were equal numbers of trials (20) in each condition, and conditions were randomised over trials. ES was asked to pick up left-side cups with the left hand and right-side cups with the right hand *regardless* of whether the handle was positioned on the left or the right side of the cup. She was asked to pick up the cups by the handle. As in all previous experiments, ES was asked to perform accurately and told that there were no time limits on responding. No feedback was given, and the instructions were repeated at frequent intervals. Performance was recorded using a video camera.

Results

The accuracy data are shown in Table 5. The cross indicates the position of the nonobject relative to midline.

Unimanual conditions. Of the unimanual conditions only one was performed well—Condition 1. Performance here did not differ from performance in the same condition in Experiments 3 and 5 [$\chi^2(2) = 0.9$, $P < .05$]. Performance in Conditions 2 and 3 was poor and did not differ significantly from performance in the same conditions in Experiments 3 and 5 [$\chi^2(2) = 5.6$, $P < .05$, and $\chi^2(2) = 2.7$, $P < .05$ for comparisons of Conditions 2 and 3 respectively across Experiments 3, 5, and 6].

The numbers of manual interference responses to handles are given in Table 11, and the numbers of grasp responses are shown in Table 12. In Condition 2 many errors were the same type as those shown in the same condition in Experiment 3; that is, on 8/15 occasions ES picked up the cup with her right hand (i.e. they were right manual interference errors). On seven occasions ES failed to pick up the cup by the handle and instead made a grasp error, lifting the cup by the base. On six of these last occasions she picked up the cup with the left (correct) hand and on one occasion with the right (incorrect) hand. These grasp errors replicate those shown in Experiment 5. In Condition 3, the error patterns were consistent—ES made left manual interference responses to the handle with her left hand on 19 occasions (similar to Experiment 3). On one occasion she made a grasp error to the base using her left hand.

Table 11. Interference Responses to Handles as a Function of the Conditions with Unimanual and Bimanual Presentations: Experiment 6 (Pick Up Upside-down Cups)

a: Unimanual Trials: Total Handle Errors 17/80

	Condition			
Hand	*1*	*2*	*3*	*4*
Left hand			19	
Right hand		8		

b: Bimanual Trials: Total Handle Errors 45/80

	Condition			
Hand	*5*	*6*	*7*	*8*
Left hand to both objects	17		1	6
Right hand to both objects		9		3
Mixed (left hand to right cup, right hand to left cup)		1		8

Unlike Experiments 3 and 5, Condition 4 was performed poorly [performance was significantly poorer than performance in the same conditions in Experiments 3 and 5; $\chi^2(1) = 8.5$, $P < .004$, and $\chi^2(1) = 5.6$, $P < .01$, for Experiments 3 and 5 respectively). All seven errors consisted of ES making a grasp error by picking the cup up from the base (six times with the left hand, once with the right hand).

Table 12. Grasp Responses to Cups as a Function of the Conditions with Unimanual and Bimanual Presentations: Experiment 6 (Pick Up Upside-down Cups)

a: Unimanual Trials: Total "Grasp" Errors 15/80 (7 with the Correct Hand, 8 with the Incorrect Hand)

Hand	*Condition* 1	2	3	4
Left hand		6	1	6
Right hand		1		1

b: Bimanual Trials: Total "Grasp" Errors 12/80 (3 with the Correct Hands)

Hand	*Condition* 5	6	7	8
Left hand to both objects	1	3	1	3
Right hand to both objects		1		
Left hand to left cup, right hand to right cup	1	2		

Bimanual conditions. The accuracy results are shown in Table 7, and the errors in Tables 11 and 12. The cross indicates the position of the nonobject relative to midline. Performance in the bimanual conditions was generally poor except for Condition 7; here performance did not differ significantly from the performance in the same condition in Experiments 3 and 5 [$\chi^2(2) = 2.6, P > .05$]. Two errors were made; on one occasion ES reached for both cups with the left hand, and on the other she picked up both cups from the base using the left hand. Performance in Conditions 5, 6, and 8 did not differ significantly from performance in the same conditions in Experiment 3 [Fisher's Exact Probability, $P = .22$, $\chi^2(1) = 9.2$, $P < .002$, and Fisher's Exact Probability $P > .99$ for comparisons of performance in conditions 5, 6, and 8 respectively in Experiments 3 and 6]. However, performance in these conditions was significantly worse than performance in the same conditions in Experiment 5 [$\chi^2(1) = 11.9$, $P < .0006$; 19.8, $P < .0001$ and 13.1, $P < .0003$ for comparisons of performance in conditions 5, 6, and 8 respectively in Experiments 3 and 5). Predominantly errors resembled those made in Experiment 3 (i.e. the orientation of the handle dictated the hand of response), although a few errors resembled those made in Experiment 5 (i.e. the cup was picked up by the base). In Condition 5, 19 errors were made; of these 17 were made by the left hand picking up first the left and then the right cup (the latter being a manual interference error). On two occasions she picked up the cups from the base, once with the appropriate hand and once with the left hand for both cups. In Condition 6, most of the errors were of the manual interference type and consisted of the right hand picking up both cups (9/16). On one occasion she performed a "cross-error", with the left hand picking up the right-side cup and the right hand picking up the left-side cup. On six occasions she picked up both cups from the bases (using the correct hands twice, the left hand only three times, and the right hand only once). In Condition 8 there were a number of different error types. On six occasions she used the left hand to pick up both cups, on three occasions she used the right hand to pick up both cups, on eight occasions she used a cross response (left hand to right cup and vice versa), and on three occasions she picked up both cups from their bases using the left hand.

Error Analysis

Summing across the unimanual and bimanual conditions, a total of 99 errors were made in Experiment 6 (representing 61.9% of all trials). However, there was a difference in error type between Experiments 3, 5, and 6. In Experiment 3 (with upright cups) the majority of errors consisted of ES responding to the orientation of the cup handle; these occurred with both left and right hands, although there were more left than right hand errors in a ratio of approximately 6:5. Similar errors were made in Experiment 6 (with inverted cups), although the proportions of the left to right hand errors differed (an approximate ratio of 3:1). However, in Experiment 5 (with cup-like nonobjects), ES mainly made left hand errors (the ratio of left:right being approximately 15:1). In Experiments 5 and 6 a substantial proportion of the errors also consisted of ES picking the cup up from the base rather than the handle; 54.8% and 27.2% of total errors in Experiments 5 and 6 respectively. Half of these were made with the correct hand and half with the incorrect hand.

Discussion

ES's performance in Experiment 6, as in the previous experiments, showed that responses were contingent on the familiarity of the object and/or the familiarity of the response. In general, performance fell midway between that in Experiments 3 and 5 in terms of both the overall level of accuracy and the number of manual interference responses that occurred. For instance, the target object(s), though familiar (cups), were presented in an unfamiliar orientation (upside-down). This had an effect of reducing the number of manual interference responses in Experiment 6 relative to those produced in Experiment 3 (although the type of response—grasping—was the same in Experiments 3 and 6). However, the familiarity of the object did have an effect on performance, since right hand performance was not as good in Experiment 6 as it had been in Experiment 5 when nonobjects had been used. Thus, the familiarity of the target object has a role in triggering response associations even when that object is presented in an unfamiliar orientation. Experiment 5 differed from Experiment 3 in that a number of errors were characterised as grasp responses; such errors never occurred in Experiment 3. A possible cause of grasp errors is that stimuli in Experiment 5 had a closed rather than an open top. In Experiment 6 the base of the cup was uppermost, and again grasp responses were seen; however, this error was not performed as frequently in Experiment 6 as it had been in Experiment 5, suggesting that learned stimulus-response associations, which are related to familiar objects, can have significant effects on performance even when the target stimulus is in the incorrect orientation.

Of particular interest was the finding that a substantial number of right hand manual interference errors were observed in Experiment 6. Similar errors had been observed in Experiment 3, leading to the suggestion that ES's right hand responses were evoked by a familiar stimulus, and in particular, were related to the orientation of the handle of the cup, rather than the location of the cup itself. The presence of right hand responses in Experiment 6 supports these conclusions; however, fewer right hand responses were produced here with inverted cups relative to Experiment 3 with upright cups; thus the familiarity of the orientation of the target influenced performance.

GENERAL DISCUSSION

We have reported an experimental study of manual interference responses in a patient with CBD. This has demonstrated that interference responses can be modulated by both the stimulus and the response context. The main findings were that:

1. Interference responses in pointing were predominantly made by the left hand and arose under conditions of spatial and response uncertainty (Experiments 1, 2, and 4).

2. When ES was required to pick objects up, interference responses were found with both hands and these were affected by the position of the relevant part of the object and the effector (e.g. the handle of the cup, Experiment 3).

3. Interference responses when picking up objects were also influenced by stimulus familiarity; fewer interference responses were generated when a cup was replaced by a structurally similar nonobject (Experiment 5) and when the cup was inverted (Experiment 6). The reduction in interference responses with less familiar objects was particularly noticeable with the right hand.
4. With cup-like nonobjects and inverted cups, some errors occurred because ES grasped the top-most part of the stimulus rather than the handle. Grasp errors were typically made with the correct hand (i.e. the hand on the same side as the object).

Factors Eliciting Right vs. Left Manual Interference Responses

ES demonstrates manual interference behaviour with both left and right hands; however, the factors eliciting the manual interference behaviour differ for the two hands. For instance, right manual interference was elicited when a familiar response was made to a familiar stimulus.

Stimulus Effects

When a familiar stimulus (a cup) had to be picked up, right hand interference responses were elicited by left-side cups providing their handle fell to the right. These were eliminated when a cup-like nonobject was used (as in Experiment 5). The orientation of the familiar stimulus was also a significant factor—fewer right manual interference responses were shown in Experiment 6 (with an inverted cup) than in Experiment 3 (with an upright cup).

Response Effects

In addition to the nature of the stimulus, the nature of the response was also important. Cups were used as stimuli in both Experiments 3 and 4 but the response differed from grasping the handle and picking up the cup in Experiment 3 to pointing to the handle in Experiment 4. Relatively few right manual interference responses occurred in Experiment 4 relative to Experiment 3. Right manual interference responses also occurred in Experiment 2a (where the task was to respond to a centrally located written cue); here it appeared that under conditions of response uncertainty, both left and right hands may be preprogrammed to initiate the required action. The manual interference shown by ES seems related to the degree of activation of response initiation processes in the right and left hemispheres. For the left hemisphere (initiating right hand movements), activation is determined by the preprogramming of responses (under conditions of response uncertainty), by the position of the relevant part of the object relative to the effector, and by familiar stimulus-response couplings.

Overall, ES was far more likely to demonstrate left manual interference rather than right, and left manual interference responses were triggered by stimuli under conditions of locational uncertainty as well as response uncertainty (Experiment 2). Left hand responses were also in general less strongly modulated than right hand responses by stimulus-response familiarity and stimulus-effector compatibility. For instance, although ES was more likely to pick up a right-side positioned cup with the left hand when its handle was on the left than when its handle was on the right (Condition 3 in Experiments 3, 5, and 6), the familiarity of the stimulus (cup vs. nonobject) or its orientation (upright vs. inverted) had little effect on performance. Furthermore, there was no difference in the number of left manual interference responses according to the nature of the response (e.g. pointing vs. grasping, Experiments 3 and 4, Condition 3). Nevertheless, the fact that the left hand performance was affected to some degree by the position of the handle of the cup does indicate that left hand responses were not simply determined by poor spatial judgements concerning stimuli on the right of ES's body. Rather it seems that the right hemisphere is strongly activated under conditions of locational and/or response uncertainty, leading to left hand responses being evoked incorrectly. Possibly due to impaired transmission across the corpus callosum, ES failed to inhibit these inappropriate responses when they were activated.

The tendency for the left hand to respond to right-side targets was so striking that we attempted to run a further experiment where ES was asked to respond to lights with the *contralateral* hand (thus, she was asked to respond to a left light with her right hand and a right light with her left hand). Interestingly, the experiment proved impossible to run. ES was completely unable to respond to the crossed location where the action was volitional, even though she made exactly these responses inappropriately in the uncrossed reaching conditions used in the present study. Hence, we conclude that her actions in our experiments were completely *involuntary*. The actions also appeared to operate outside conscious awarenesss, since ES was typically unaware when an incorrect response was made and thought that she had responded correctly. This was the case for all the current experiments. We return to this last point when we discuss the relations between ES's performance and neuropsychological categories of anarchic and alien hand syndromes.

Action Selection

The differential effects of the stimulus and response factors on left and right hand performance in ES are important for understanding how actions to visual stimulus are evoked and selected. Distinctions have been made previously between the dorsal and ventral streams of visual processing in the brain. The dorsal stream is largely thought to subserve spatial vision and action whereas the ventral stream is more implicated in object recognition (Ungerleider & Mishkin, 1982). Neuropsychological data have supported this distinction. For example, Milner, Goodale, and associates have reported an agnosic patient who, after a ventral lesion, was unable to perform simple perceptual matches (e.g. requiring same/different matching of object size) but who was nevertheless able to make the appropriate grasp aperture with the same stimuli, presumably due to the integrity of the dorsal route to action (Goodale, Milner, Jakobson, & Carey, 1991; Milner & Goodale, 1995; Milner et al., 1991). The dorsal stream appears to play a critical role in the visuomotor transformations necessary for skilled visuomotor acts, but to be relatively indifferent to the nature of the stimuli involved (e.g. whether they are familiar or unfamiliar objects (Milner & Goodale, 1995). However, action can also be affected by the familiarity of objects. Jeannerod, Decety, and Michel (1994) report data from a patient with bilateral parietal lesions who showed a contrast between reaching and grasping familiar and unfamiliar objects. With familiar objects, grasp apertures were scaled to the size of the stimuli; with unfamiliar objects, grasp apertures were scaled inaccurately to object size.

Other evidence suggests that actions evoked by familiar objects may be dependent either on the activation of semantic knowledge concerning an object's use, or directly from stored visual knowledge concerning the object (e.g. a direct route from a stored structural description of an object to an action). Direct links between stored visual knowledge and actions can be apparent in patients with optic aphasia. For instance, Riddoch and Humphreys (1987) reported one such patient who was impaired on tests assessing visual access to semantic knowledge, but who nevertheless performed very specific gestures when objects were visually presented (see also Hillis & Caramazza, 1995). Such data suggest that specific learned gestures can be evoked directly via access to stored visual knowledge, even when access to semantic knowledge is impaired. An opposite pattern of results arises from "visual apraxia". Here patients may very well be able to make actions semantically, for instance, from the object's name. However, such patients are impaired at making actions when objects are visually presented. Here there seems to be a "blocking" of action from directly accessed visual information (see Pilgrim & Humphreys, 1991; Riddoch, Humphreys, & Price, 1989). Blocking of the response may not only come from stored visual knowledge but also from several possible responses that may be "afforded" by the parts of objects (e.g. that are not modulated by stored visual knowledge).

The data we have obtained from ES supports the view that actions with the right hand are influenced by the familiarity of the stimulus and its associated response. The results also extend prior findings by demonstrating effects of the familiarity of the object's orientation and the orientation of the object with respect to the relevant effector (e.g. whether the handle of the cup was on the left or right). Visual object recognition itself seems relatively indifferent to the left–right orientation of the object (Biederman & Cooper, 1991), and the semantic information retrieved from objects will be the same irrespective of the way the objects face. Nevertheless, ES's performance was strongly affected by the left–right orientation of the cups. This suggests that right manual interference responses were not generated on the basis of semantic information accessed by the objects, but rather this activity was contingent on direct links between vision and action. The fact that right manual interference responses were sensitive to the particular object (being evoked by cups but not by nonobjects) further suggests that these actions were contingent on stored visual knowledge being activated, although the specificity of the stored knowledge is less clear. It may be that the presence of a handle on the right side of a cylindrical container, when the task is to grasp the object, may be sufficient to trigger a right hand response. There need not be access to stored knowledge specific to the particular cup. Whatever the case, the results show that the visual representations involved are sensitive to object orientation.

In addition to the effects of familiarity, ES's right manual interference responses were influenced also by (a) the spatial compatibility between the parts of objects used for action and the effector, and (b) the goal of the action (reaching or pointing). Right manual interference responses occurred primarily when the cup's handle was facing right, and they arose when the task was to pick up rather than point to the object. These effects, of object part–hand compatibility and goal-state, demonstrate that visual affordances affect action. The ecological psychologist J. J. Gibson (1979) argued that visually guided behaviour depends on direct links (or affordances) between perception and action. The affordance of an environmental stimulus may be defined in terms of the relation between the visual information present and the goal of the organism; for instance, if a surface is flat, reasonably substantial and of an appropriate height, it will "afford" sitting on to the tired observer whether it has been specifically designed for this (e.g. a stool), or "happens" in the environment (e.g. a tree stump). In the experiments reported here, the position of the handle on the cup will more directly afford lifting by one hand than the other (i.e. a right-side handle for the right hand), leading to stronger activation of the response system for that hand. This activation seems particularly strong for the right hand. In the absence of inhibitory signals to the response system, incorrect hand responses are generated. Incorrect responses were not generated, though, when the task goal changed from picking up the cup by the handle to pointing to the cup handle. Thus, the critical object part did not "afford" action when the task did not require picking the object up. We suggest that, for ES, the inhibition of inappropriately activated responses is disrupted by reduced callosal transmission and/or that the frontal motor systems which generate action in response to volitional cues are deficient in some way (either in the nature of the inputs to them, or the systems themselves are damaged).

The left manual interference responses in ES were most affected by locational and response uncertainty, and less affected by stimulus similarity. This dissociation between the right and left hand suggests that the computational processes involved in programming the spatial parameters of actions reside within the right hemisphere and are separated to some degree from processes sensitive to stimulus-response familiarity in action, within the left hemisphere.

Grasp Responses

Other evidence supportive of the role of affordances in directing action comes from the grasp errors found in Experiments 5 and 6. In these experiments, ES was presented with relatively unfamiliar stimuli: cup-like nonobjects and inverted cups. Along with manual interference responses to the handles of these stimuli, ES also made some grasp errors, where she picked the object up (incorrectly) by their topmost part rather than the handle. Interestingly, these responses were often made with the correct hand (on the same side as the object). Since the objects were less familiar in these experiments, responses might tend to be based on affordances rather than learned object–action associations. With cup-like nonobjects and upside-down cups, affordances may be as strong from the top of the object as from the handle. Note, however, that the top has no spatial component linked to the hand of response (unlike the handle). In this case, the strongest affordance should be to the hand nearest the object rather than the opposite hand. As a result, grasp responses are made using the correct hand.

Neurology

On the basis of studies of the movement disorders (apraxias) resulting from left hemisphere lesions, Liepmann (1920) argued that the left hemisphere in right-handed individuals is dominant in the control of some aspects of purposeful skilled movement. In particular, the left hemisphere controlled movement that had to be performed in response to a verbal command, or where imitation of an examiners movement was required. For such actions, the left hemisphere was proposed to control the right hand directly and the left hand via transcallosal links. However, the right hemisphere may house some abilities to generate learned movements to visually presented objects or to objects in naturalistic contexts. Support for this last hypothesis comes from a number of case reports of patients with left hemisphere or callosal lesions who have retained some of the practical functions of the left hand (see Rapcsak, Ochipa, Beeson, & Rubens, 1993). Rapcsak et al. report the practic functions of a man whose left hemisphere was almost completely destroyed as a result of a massive left-hemisphere stroke. Although the patient was severely impaired in gesture imitation and gesture to command, his ability to perform overlearned habitual actions with real objects and intransitive gestures (such as waving goodbye, or shaking a fist) was relatively unimpaired. A somewhat similar proposal has been put forward by Buxbaum, Schwartz, Coslett, and Carew (1995), who also argue that different mechanisms may underlie gesture and naturalistic action; however, they propose that naturalistic action requires the specialised abilities of each hemisphere, integrated across callosal structures. The left hemisphere may be dominant for learned hand gestures especially when performed out of context (with single objects); the right hemisphere may be dominant for control of the spatial parameters of movements. Buxbaum et al.'s proposal is supported by data from a patient with callosal disconnection syndrome following a closed head injury. Although the left hand was particularly impaired on standard gesture tests (suggesting disconnection from the left-hemisphere control systems) both hands performed abnormally in everyday action tasks. The right hand then frequently made spatial errors, whilst the left hand frequently misused objects. ES has a bilateral disturbance of manual performance. It is possible that this may be associated with callosal dysfunction (signal abnormalities are shown on MRI in the region of the posterior centrum-semiovale and the corpus callosum on the left). Impairment in this area would disrupt the axons mediating interhemispheric integration.

Our data show that it is not sufficient to attribute the manual interference behaviour in ES simply to a deficit in fine motor control with the nondominant hand; rather, ES has a problem in modulating activation from stimulus-driven responses to stimuli in response to task demands. This is consistent with a failure to inhibit activation in brain regions in the contralateral hemisphere responsive to stimulus-drive action, possibly as a result of impaired links across the corpus callosum. The left hemisphere may be critical for "abstract" aspects of action (i.e. the ability to gesture the use of an object in its absence, or to imitate an examiner pantomiming an action) (Liepmann, 1920; Rapcsak et al., 1993). ES was shown to be particularly poor at imitating gestures produced by an examiner (see Fig. 1); gesturing the use of an object to command, although not so impaired as gesture imitation, was still performed very poorly. These aspects of ES's performance suggest an impoverished ability for her left hemisphere to generate action. Nonetheless, an influence of left-hemisphere activation on performance was apparent because right hand actions, in particular, were affected both by the familiarity of the stimulus and its associated response. Inappropriate right hand responses were generated when learned responses had to be made to familiar stimuli ("pick up the cup"). This may be because the left hemisphere may be dominant for such responses, although the right hemisphere may be able to initiate them to some degree. In contrast, inappropriate left hand responses may be generated under conditions of spatial uncertainty because the right hemisphere dominates control of the spatial parameters of movement, and is the more strongly activated hemisphere under these conditions. ES appears to be unable to integrate activity across the hemispheres, and there seems to be little inhibition from one hemisphere of inappropriate responses activated in the other—manual interference behaviour results. Overall, more manual interference behaviour was observed with the left rather than the right hand, which probably reflects the greater degeneration of the left hemisphere. In both cases, however, the stimulus driven nature of the deficits suggests some disconnection of the system controlling voluntary action (e.g. SMA) from areas responsive to environmental stimuli (e.g. PMC)—(see the Introduction). This may be a consequence of subcortical damage in ES's case.

Anarchic Hand Syndrome and Utilisation Behaviour

There were manual interference effects and inappropriate actions during everyday life that ES was aware of. The question arises, then, whether the manual interference responses that we have studied experimentally form part of this syndrome. This situation is not clear. One of the critical defining features of anarchic hand syndrome, namely awareness of the incorrect action, was not apparent in our study. ES showed no awareness of making incorrect manual interference responses. This suggests that the interference responses we elicited may arise from a source separate to the source of her action errors in everyday life. On the other hand, the consequences of some of the action errors that befell ES in everyday life could be severe (as when her left hand hit her aunt!). In our experiments, though, there were no adverse consequences for making a manual interference response, and in some respects the goal of the task was fulfilled: ES pointed to or picked up the target object. Speculatively, we might suggest awareness of inappropriate actions in anarchic hand syndrome actually reflects the *consequences* of actions rather than observations of the inappropriate actions per se. In this last case the present manual interference responses may in fact be part of the anarchic hand syndrome in this patient. The "awareness" shown by patients labelled as having anarchic hand syndrome may apply only to consequential acts noted in the clinic. We do not know whether more subtle motor deficits of the type we have examined could be detected in all such patients.

Are the manual interference affects described here with ES the same as utilisation behaviour associated with frontal lobe damage (see Shallice, Burgess, Schon, & Baxter, 1989)? In their formal investigations of a patient with an acute behavioural disturbance[1] as a result of lesions in the distribution of branches of both anterior cerebral arteries, Shallice et al. describe three different forms of utilisation behaviour. Toying (a single action in which an object is manipulated but not in a purposeful way, or in the way it was originally tended to be used; e.g. picking up a pencil but not using it for anything); complex toying (two objects used together in a linked way but in an incomplete fashion or not for the purpose for which they were both designed); and coherent activity (a set of actions integrated in a typical fashion with respect to the objects involved such as picking up a pen and paper and writing). Utilisation behaviour occurred not only when the patient was in conversation with the examiner, but also when he was in the middle of performing both verbal and nonverbal tasks (Shallice et al., 1989). It seems to us that the manual interference effects we have described and utilisation behaviour are not the same thing. The laboratory circumstances for ES and for Shallice et al.'s patient were not comparable (for our experiments only the test items were present); however, ES was never observed to perform utilisation behaviours with other items in situations where other objects were available but inappropriate to the task in hand (such objects present on the table whilst we were performing the neuropsychological assessments). Indeed, in formal tests, ES can reject distractor objects and responds only to targets (even if the response is then inappropriate (Riddoch, Humphreys, & Edwards, in press). Futhermore, even in the present study, ES was able to maintain task goals at some level. For instance, she was required to grasp mugs in Experiment 3, but to point to the handle of the mug in Experiment 4. Here she responded appropriately according to the task set, unlike patients showing utilisation behaviour.

The manual interference effects we have reported here thus may be part of the anarchic hand syndrome in this patient but they dissociate from utilisation behaviour. Manual interference effects can occur under conditions in which patients maintain appropriate task goals, and they are influenced by (a) spatial uncertainty concerning the response (particularly of the left hand) and (b) stimulus familiarity and orientation, when the stimulus orientation is relevant to the task goals (particularly for the right hand). This last property demonstrates that visual affordances play a part in the selection of action to objects.

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[1] On 17 September, 1987, his son reported that the patient was found early in the morning wearing someone else's shoes, not apparently talking or responding to simple commands but putting coins into his mouth and grabbing imagineary objects. He went round the house, moving furniture, opening cupboards and turning light switches on and off.

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