

Don't think twice, it's all right—contralesional dependency for bimanual prehension movements

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Abstract

In bimanual coordination when moving the hands to two separate objects, subjects tend to initiate and terminate the movements together, even when the targets are at different distances or are of a different size. Additionally, each hand tends to scale its grasp independently to the object to be grasped. Here, we report the performance of a patient, who had previously shown signs of motor neglect, on two experiments investigating coupling and independence in bimanual coordination. The patient showed relatively normal bimanual behaviour for the transport phase of prehension when objects were placed at different distances (Experiment 1), but abnormal behaviour for the grasp component when objects were of different sizes (Experiment 2). Moreover, the contralesional limb demonstrated a dependency of grasp that was related to the object grasped by the ipsilesional limb. We discuss the possible underlying mechanisms of this dependency in relation to competitive motor programming and attentional bias. The results also reinforce the view that the transport and grasp components of prehension are distinct processes.

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1. Introduction

The ability to coordinate movements of the two hands during functional activities is a remarkable skill that humans and other primates have developed. Many varied skills (e.g. using a tin-opener, playing a piano) demonstrate both the independence of the two limbs and also the cooperation between them. In recent years, we have witnessed a rapid expansion in our understanding of the relationship between the hands at both behavioural and neural levels. For example, when the hands move to targets of variable distance and direction, there appears to be strong coupling of the limbs with almost synchronous movement onsets, times to peak velocity and movement end, despite the hands moving at different speeds (Kelso, Southard, & Goodman, 1979).

The performance of bimanual reach-to-grasp movements presents potential dilemmas for the organising system, es-

pecially when the targets are of differing distances or different sizes. For instance, can subjects independently scale velocity to two targets of differing distance, or independently shape each hand to targets of differing size while maintaining synchrony between the two limbs in terms of movement onset and end? The evidence appears to suggest that they can. Castiello et al.'s initial work on bimanual reach-to-grasp movements demonstrated that subjects tend to synchronise movement onset and movement end points when moving to targets of differing sizes, while maintaining independent shaping of each hand based on the relative size of the target (Castiello, Bennett, & Stelmach, 1993). However, not all temporal parameters were coupled. It was found that the hand moving towards the smaller target, reached the point of peak velocity earlier than the hand moving towards the larger target and had a longer deceleration period. It is notable that in this study, subjects made a 'whole hand' grip to the large target while making a 'precision' grip to the small target. More recent work investigating bimanual reach-to-grasp movements to different sized targets has shown close cou-

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pling of all the major temporal parameters (movement onset, time to peak velocity, time to peak grip aperture, movement end) (Jackson, Jackson, & Kritikos, 1999). However, in line with the above study of Castiello et al. (1993), shaping of the hand was found to be independent for each hand relative to the target to-be-grasped. This particular aspect of bimanual movements appears to be robust, being further replicated in a study by Dohle, Ostermann, Hefter, and Freund (2000). However, the finding may be task-dependent. Further work by Jackson, German, and Peacock (2002) has shown that when two different sized targets are 'unified' so that they appear to be part of the same object, the hands show a reduced level of independence. That is, the hand moving towards the larger target shapes smaller and the hand moving towards the smaller target shapes larger, relative to when the targets are not 'unified'. It should be noted however, that the change, while significant, was relatively small with the hand moving towards the smaller target shaping much smaller than the hand moving towards the large target, independent of 'unification'.

When the two hands move to two targets differing in distance, there is again synchronisation of onset and endpoints (Kelso, Putnam, & Goodman, 1983). To achieve this synchronisation, it is necessary for the subject to scale the velocity profile of each hand appropriately (slower to the near target, faster to the far target). This very synchronisation, however, leads to the violation of Fitts' Law, which predicts that movement duration is affected by the distance moved and the precision required by the size of the target, these components leading to a particular index of difficulty (Fitts, 1954). As the target becomes smaller or moves further away, the index of difficulty rises; as the target gets closer or becomes larger, so the index of difficulty reduces. Interestingly, when moving to targets of mixed difficulty, one might assume the movements to synchronise to the movement with the lowest index of difficulty. However, this does not appear to be the case. Kelso et al. showed that the movement with the higher index of difficulty moved faster and the hand with the lower index of difficulty moved slower in order to achieve the synchronisation (Kelso et al., 1979). This finding has been shown to be true for bimanual reach-to-grasp movements also (Jackson et al., 1999).

Nevertheless, though aspects of bimanual movements are usually coordinated, there are also typically costs to performance. For example, relative to unimanual movements, bimanual reach-to-grasp movements are slower (peak velocity), take longer (movement duration) and shape larger (peak grip aperture) (Jackson et al., 1999). These changes may represent the level of certainty involved in computing and controlling the movements as the degrees of freedom for the unimanual movements are doubled for bimanual actions. This cost for bimanual movements is typically borne by both hands. Thus, the peak grip aperture of both hands increases under bimanual conditions compared to unimanual movements (Jackson et al., 1999).

The performance of bimanual movements is also affected by attention. For example, bimanual movements are slower and less stable when carried out under dual task conditions (Monno, Temprado, Zanone, & Laurent, 2002). Also, performance is affected by directing attention to one of the hands involved. During bimanual circle-drawing, synchrony is optimised when attention is directed to the dominant hand, while non-dominant hand movements are more accurate when attention is directed towards it (Swinnen, Jardin, & Meulenbroek, 1996; Wuyts, Summers, Carson, Byblow, & Semjen, 1996). However, a recent study of bimanual reach-to-grasp movements showed no effect of directing visual attention towards one target (Jackson et al., 2002). Movements remained tightly synchronised while each limb expressed independence for the size of target to be grasped.

Based on the above findings, one might expect that patients with attentional deficits would have difficulties with bimanual movements. Recently, evidence from bimanual hand circling in patients with parietal lesions has suggested that the specific role of the parietal lobe in directing attention may account for this abnormal performance (Serrien, Nirkko, Lovblad, & Wiesendanger, 2001). Three patients with left parietal lesions showed a lag of the contralesional limb that worsened with task difficulty. Additionally, Jackson et al. (2000) studied a patient with a right parietal lesion (DB) on a bimanual prehension task and showed inappropriate coupling of peak velocity of the contralesional limb when bimanual movements were made to targets at different distances. The authors attribute this finding to severe hemianaesthesia of the left side, which reduced the proprioceptive cues available for DB to control the movement. It is also possible, though; that some abnormal interactions between the hands for DB may reflect an attentional bias that affects motor performance. This was examined here in the study of a patient with (recovered) motor neglect.

Patients with motor neglect are able to move their affected limbs relatively normally when prompted to do so, but show an under-use under normal conditions when the ipsilesional limb is favoured. The problems of the contralesional limb may also be exacerbated under bimanual conditions, perhaps due to competition between the hands in effecting a motor programme, generating a pattern of 'motor extinction' (Valenstein & Heilman, 1981; Meador, Watson, Bowers, & Heilman, 1986). Reports of motor extinction are few but case studies of patients who showed motor extinction for movement initiation (hypokinesia) do exist (Valenstein & Heilman, 1981; Meador et al., 1986), together with more recent accounts for impersistence (Mattingley & Driver, 1997; Mattingley, 2002). Motor extinction may be thought of as an analogue of perceptual extinction, a relatively well recognised deficit within the neglect syndrome (Driver & Vuilleumier, 2001). Two problems emerge when attempting to identify patients with motor neglect or extinction. Firstly, the diagnosis is a clinical one, based on observation of the patient's behaviour and to date there are no specific, recog-

nised tests as there are for visual neglect. Secondly, many patients with spatial neglect have concurrent hemiparesis, rendering the ability to test for a neglect-related deficit impossible. Nevertheless, there is a growing recognition that primary motor deficits (e.g. hemiparesis) may be masking motor neglect in many patients (Robertson, McMillan, MacLeod, Edgeworth, & Brock, 2002; Vallar, Bottini, & Sterzi, 2003).

Here, we report data on bimanual reach-to grasp movements in a patient who was clinically identified post-stroke as having motor neglect and extinction. The two experiments were based on those previously performed on normal subjects (Jackson et al., 1999). In Experiment 1, the distance of the two targets was manipulated to investigate independence of the two limbs for the transport phase of reaching-to grasp. In Experiment 2, the size of the targets was manipulated in order to investigate independence of the limbs in the grasp phase. Jeannerod (1981) first proposed that reach-to-grasp movements are “organised on the basis of separate motor components corresponding to dissociable sensory channels and perceptual descriptions” (page 155). These separate motor components are involved in the control of ‘transport’ and ‘grasp’ components of movement. Thus, changing the location of an object alters the transport but not the grasp component of an action (Chieffi, Gentilucci, Allport, Sasso, & Rizzolatti, 1993), while object size affects grasp but not necessarily the transport component (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994). Though the functional separation between the reach and grasp components of movement should be supported by an underlying neurological separation, there are few neuropsychological data supporting this. Jeannerod, Decety, and Michel (1994) did report a selective impairment for the grasp component with normal transport kinematics in a patient with bilateral parietal damage. However, to our knowledge a double dissociation has not been observed, which sheds doubt on whether the two components are represented by distinct neural substrates. This was tested here by comparing bimanual coupling between, respectively, the reach and grasp components of the task. We report a dissociation between relatively preserved bimanual actions for the transport component (Experiment 1), and impaired bimanual actions (contralesional dependency) for the grasp component (Experiment 2). The data emphasise the distinction between these components of action.

2. Case report

MM, a 75-year-old right-handed woman was admitted to hospital having suffered a cerebrovascular accident in December 2001. A CT scan revealed infarction in the region of the right middle cerebral artery affecting the inferior frontal gyrus, the middle frontal gyrus and the superior temporal gyrus (see Fig. 1). She had a mild hemiparesis and demonstrated motor neglect, an underuse of the contralesional limbs.

This was most obvious in the initial weeks after stroke when MM appeared to have total paralysis of the contralesional (left) arm and yet used the arm relatively normally when specifically asked to use it. Motor neglect was also apparent during gait, when MM would tend to ‘drag’ the left leg but walked relatively normally when reminded to step the left foot. At this time, neurological examination revealed the following information. Muscle power was 4/5 on the left and 5/5 on the right (MRC scale). Assessment of tone showed no abnormalities with equal tendon reflexes left and right. Plantar responses were downward bilaterally and there was no clonus. She made a good recovery and was largely independent in tasks of everyday living. This study was undertaken 6 months following MM’s stroke in June 2002.

At the time of the current tests of motor performance, MM scored at ceiling on the star cancellation, line cancellation and letter cancellation subtests of the Behavioural Inattention Test (Wilson, Cockburn, & Halligan, 1987). She also performed at ceiling when examined using confrontation for visual extinction (10 left, 10 right and 10 bilateral stimuli presented). In order to ‘push’ this further, MM was tested on the Posner Cueing Paradigm (Posner, Inhoff, & Friedrich, 1987). Here, MM performed well (see Fig. 2) and, while responding marginally slower to contralesional targets, was not abnormally affected by ipsilesional cues occurring prior to contralesional targets¹. MM did show a degree of tactile extinction showing contralesional extinction on 4 out of 10 presentations of bilateral light touch stimuli to the hands. Proprioception was intact for both hands when tested for movement detection and discrimination but MM had difficulties in limb matching (examiner moves contralesional limb and subject moves ipsilesional limb to the same ‘mirrored’ position). However, this particular test, while clinically popular, appears to confound the relative contributions of proprioception and attention and as such should be interpreted with care. MM was also tested on a novel test of motor extinction both shortly following stroke and at the time of this study. She was asked to tap as quickly as possible using WPS Electronic Tapping Tests (WPS ETT). Shortly following stroke, when tapping with the right hand unimanually, MM registered 46 taps in a 10 s period, compared with 44 left hand taps. However, when tapping bimanually she registered 44 taps with the right hand but only 19 with the left. When repeated on the task at the time of this study, MM made equivalent numbers of taps with the left and right hands both unimanually and bimanually. Thus, motor extinction was reduced at the time of testing, though it could still contribute to bimanual performance under more taxing motor conditions (reaching and grasping objects, as here).

¹ MM responded slower to contralesional targets (mean = 582 ms) than ipsilesional targets (mean = 495 ms) but crucially did not show a significant Side \times Validity interaction ($F(1, 286) < 1.0, p = 0.7$) indicative of visual extinction.

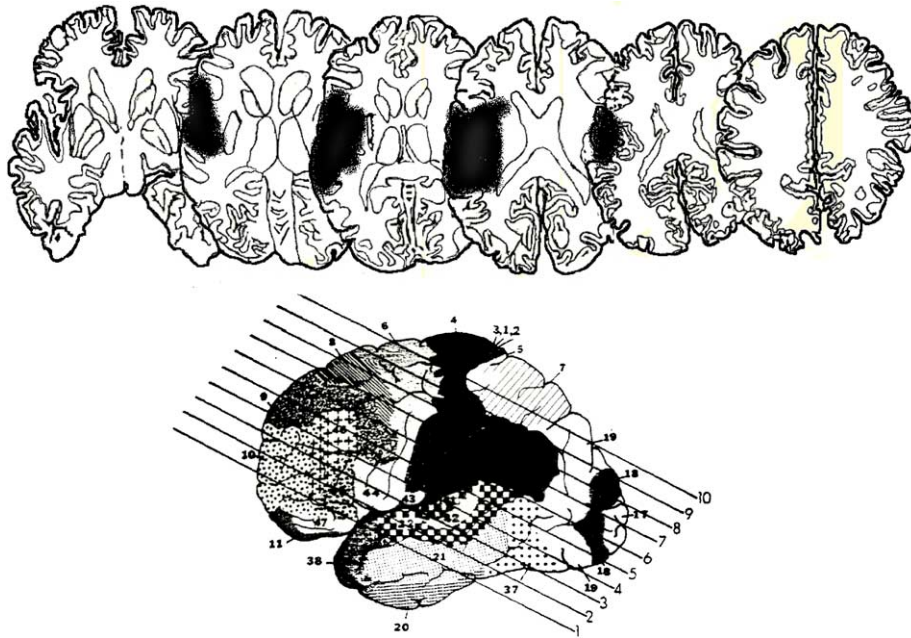


Fig. 1. Lesion reconstruction for MM, from CT scan. The lesion has been drawn onto standard slices from Gado, Hanaway, and Frank (1979). The bottom figure shows the 10 slices used. Only slices 3–8 are depicted here. The left of each slice represents the right hemisphere.

3. Experiment 1

In Experiment 1, we examined the ability of MM to scale the transport component of reach-to-grasp movements by comparing unimanual with bimanual movements. In addition, for bimanual movements, we examined both congruent (target of equal distance away) and incongruent (targets placed at different distances) movements. We hypothesised

that MM may inappropriately couple the velocity profiles of her two hands to incongruent targets as described above for DB (Jackson et al., 2000).

3.1. Method

MM was asked to make either unimanual or bimanual movements to targets placed at positions on the table in front of her (see Fig. 3). Each trial began with both of MM's hands resting on the table with the thumbs and index fingers gently resting around small cylinders fixed to the table. Targets (cylinders 6 cm in diameter and 2 cm deep) were placed either 15 cm or 30 cm directly in front of each hand. On unimanual

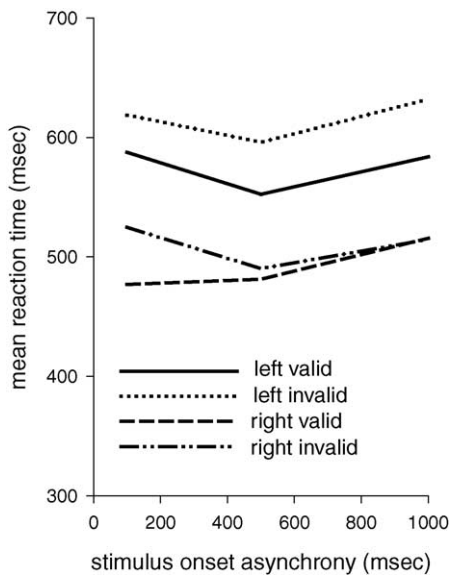


Fig. 2. MM's results on the valid vs. invalid cue paradigm (Posner et al., 1987). While reaction times were slightly slower to contralateral targets, the typical severe slowing to contralateral targets following an ipsilateral cue was not observed.

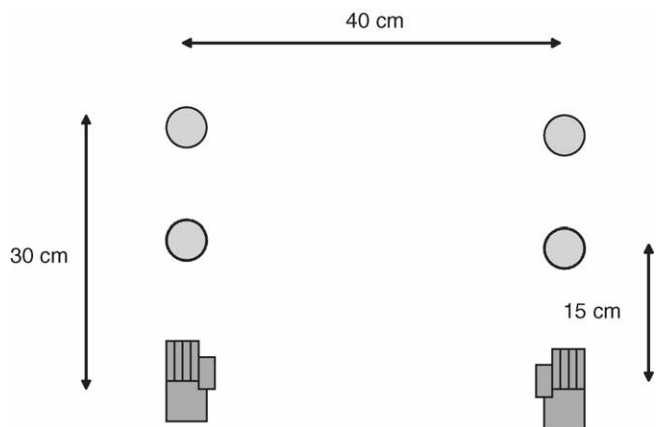


Fig. 3. Set-up for Experiment 1. MM made unimanual reaches to either near or far targets, bimanual congruent reaches (far/far; near/near) or bimanual incongruent reaches (near/far; far/near).

trials, a single target was presented; on bimanual trials, two targets were presented. When cued to move by a ‘beep’, MM reached ‘quickly but accurately’ to the targets. Each trial was presented in full vision of the subject and it was introduced by the experimenter (“this time there is a near target on the left and a far target on the right”, or, “this time there is just a far target on the right”, etc.). Conditions were presented randomly over trials and MM performed 10 repetitions for each of the 8 conditions (unimanual: left near, left far, right near, right far; bimanual: congruent near, congruent far, incongruent left near right far and incongruent left far right near). The movements were measured using a 3D motion tracking system (ProReflex, Qualysis Ltd.), sampling at 100 Hz. Reflective markers were placed on the nail of the thumb and index fingers, the radial head at the wrist and on each of the targets (the target markers were not visible to the subject).

3.2. Results

Movement parameters were chosen and calculated using customised software (QTools, Qualysis Ltd.), defined as:

Movement onset—this was taken as the first frame in which wrist marker velocity consistently exceeded 50 mm/s.

Movement end—first frame in which target marker position moved 1 mm.

Movement duration (MD)—movement end time minus movement onset time.

Peak velocity (PV)—the highest velocity value reached during the prehension movement.

Time to peak velocity (TTPV)—the frame in which PV was reached.

Peak grip aperture (PGA)—the maximum distance found between the index finger and thumb markers during the movement.

Time to peak grip aperture (TTPGA)—the frame in which PGA was reached.

Deceleration time—movement end time minus TTPV.

The individual parameter values calculated in all the analyses were treated as individual subjects. Table 1 shows the mean kinematic parameters for each hand in all conditions. An independent subjects $2 \times 2 \times 3$ ANOVA was conducted containing the following factors: hand (left, right); distance

(near, far) and condition (unimanual, bimanual congruent, bimanual incongruent).

3.2.1. Kinematics for the transport phase

3.2.1.1. Movement duration. Movements to ‘far’ targets were longer than those to ‘near’ targets (near = 717 ms, far = 859 ms, $F(1, 78) = 19.0$, $p < 0.0001$). There was also a significant main effect of condition ($F(2, 78) = 10.2$, $p < 0.0005$). Unimanual movements (682 ms) were significantly shorter than both bimanual congruent movements (876 ms, $F(1, 78) = 18.4$, $p < 0.0001$) and bimanual incongruent movements (817 ms, $F(1, 78) = 11.6$, $p < 0.005$). However, the two bimanual conditions were equivalent ($F(1, 79) = 1.0$, $p = 0.3$). Left hand movements took slightly longer than right hand movements (left = 821 ms, right = 765 ms, $F(1, 78) = 4.3$, $p = 0.04$). None of the two-way or three-way interactions approached statistical significance.

3.2.1.2. Peak velocity. The left and right hands had equivalent values for peak velocity (left = 554 mm/s, right = 572 mm/s, $F(1, 93) < 1.0$, $p = 0.4$). Peak velocity was higher for targets that were further away than for targets that were closer (near = 457 mm/s, far = 660 mm/s, $F(1, 93) = 114.3$, $p < 0.0001$). There was a significant main effect for condition ($F(2, 93) = 16.5$, $p < 0.0001$). Peak velocity for unimanual movements (630 mm/s) was significantly higher than both bimanual congruent movements (540 mm/s, $F(1, 93) = 17.8$, $p < 0.0001$) and bimanual incongruent movements (513 mm/s, $F(1, 93) = 29.3$, $p < 0.0001$). However, the two bimanual conditions were equivalent ($F(1, 93) < 1.0$, $p = 0.3$). There was a significant Hand \times Distance interaction ($F(1, 93) = 8.0$, $p < 0.01$) with the left hand on average tending to have a higher peak velocity to near targets and a lower peak velocity to far targets than the right hand (Fig. 4).

3.2.1.3. Time to peak velocity. Across the experiment, the left hand took longer to reach peak velocity than the right hand (left = 407 ms, right = 311 ms, $F(1, 79) = 27.1$, $p < 0.0001$). A Hand \times Condition interaction was marginally significant ($F(2, 79) = 3.0$, $p = 0.06$) with unimanual movements largely accounting for the difference in the hands. As can be seen from Fig. 5, TTPV for bimanual incongruent movements

Table 1
Mean kinematic values for Experiment 1

	Unimanual				Bimanual—congruent				Bimanual—incongruent			
	Near		Far		Near		Far		Near		Far	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Duration (ms)	676	575	834	636	769	734	949	974	753	769	931	814
Peak velocity (mm/s)	503	511	680	833	477	429	614	609	439	371	578	646
Time to peak velocity (ms)	396	260	419	268	427	264	426	333	355	350	425	354
Deceleration time (ms)	294	292	446	374	494	623	523	641	414	419	469	450
Peak grip aperture (mm)	145	123	141	125	141	122	143	129	146	129	147	128
Time to peak grip aperture (ms)	334	400	407	465	436	488	521	658	436	531	583	581

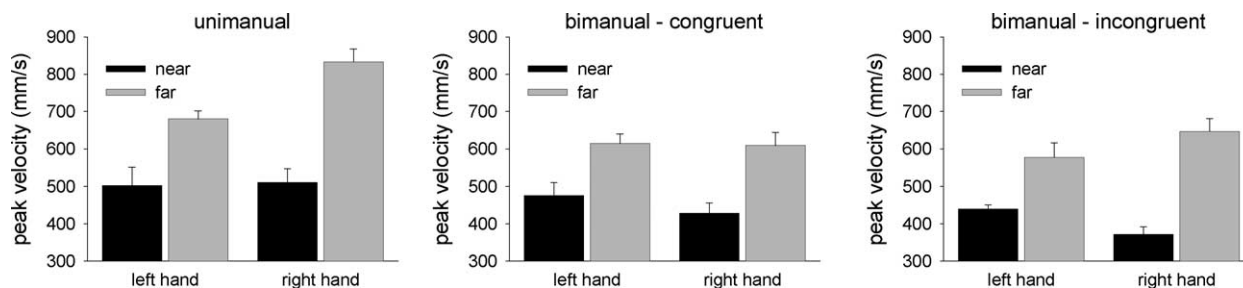


Fig. 4. Mean peak velocity values across the three conditions in Experiment 1.

tended to be well coupled. No other main effects or interactions approached significance.

3.2.1.4. Deceleration time. There was a significant main effect for condition ($F(2, 95) = 9.1, p < 0.0005$). Contrasts showed that unimanual movements (353 ms) had significantly shorter deceleration times than bimanual congruent movements (572 ms, $F(1, 95) = 18.3, p < 0.0001$) but not bimanual incongruent movements (439 ms, $F(1, 95) = 3.0, p = 0.09$). Bimanual incongruent movements had significantly shorter deceleration times than bimanual congruent movements ($F(1, 95) = 6.5, p < 0.05$). None of the other main effects or interactions reached statistical significance.

3.2.1.5. Temporal coupling of the transport phase. In addition to the above, we also examined the coupling of the hands on bimanual trials for movement onset and movement endpoint both in terms of the 'lag' (left hand–right hand)

and the correlation between the limbs. For Experiment 1, the mean movement onset lag was -74 ms demonstrating that the left hand tended to initiate the movement before the right hand. However, the time lag was relatively small and the movement onsets were ostensibly well coupled. Furthermore, movement onset lag did not differ significantly between the two bimanual conditions (means: congruent = -67 (15) ms; incongruent = -82 (14) ms; $F(1, 26) < 1.0, p = 0.5$). In addition, a significant correlation was found between the left and right hands for movement onset ($r = 0.9, p < 0.0001$).

The mean movement endpoint lag was -38 ms again suggesting close coupling between the limbs. Lags did not vary significantly between conditions (means: congruent = -49 (33) ms; incongruent = -27 (30) ms; $F(1, 35) < 1.0, p = 0.6$) and were significantly correlated ($r = 0.8, p < 0.0001$).

For the transport phase, MM was clearly able to couple her hands appropriately and she also scaled peak velocity appropriately for the bimanual incongruent condition.

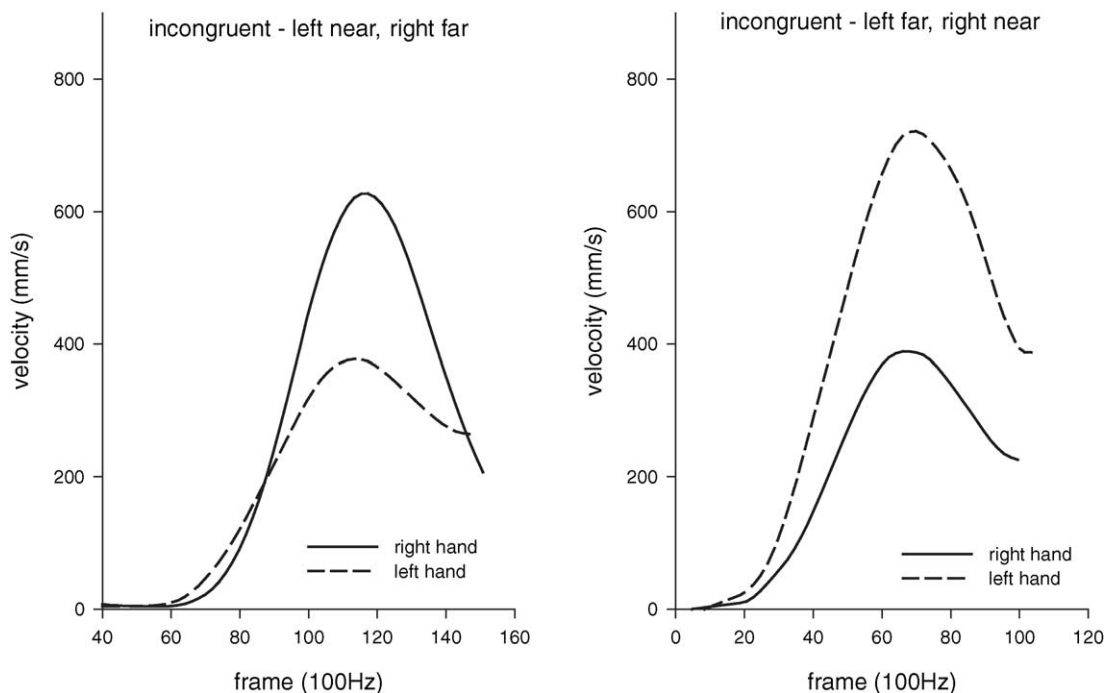


Fig. 5. Representative velocity profiles for the right and left hands for the incongruent conditions in Experiment 1. These profiles show the normal scaling of peak velocity and the tight coupling of movement onset, time to peak velocity and movement end. Peak velocity for the left and right hands varies according to which object is more distant.

3.2.2. Kinematics for the grasp phase

3.2.2.1. Peak grip aperture. There was a significant main effect for hand ($F(1, 105) = 142.4, p < 0.0001$), the left hand (mean = 144 mm) shaping larger than the right hand (mean = 126 mm). No other main or interaction effects reached significance.

3.2.2.2. Time to peak grip aperture. The left hand reached peak grip aperture significantly earlier than the right hand leading to a main effect for hand (left hand = 454 ms, right hand = 530 ms; $F(1, 78) = 7.8, p < 0.01$). Movements to near targets reached peak grip aperture earlier than those to far targets (near = 438 ms, far = 540 ms; $F(1, 78) = 16.5, p < 0.0005$). There was also a main effect for condition ($F(2, 78) = 12.3, p < 0.0001$). Contrasts revealed that in the unimanual condition (mean = 401 ms) the peak grip aperture was reached significantly faster than in both the bimanual conditions (congruent = 537 ms; $F(1, 78) = 17.1, p < 0.0001$; incongruent = 531 ms; $F(1, 78) = 20.4, p < 0.0001$). There was no significant difference between the two bimanual conditions ($F(1, 78) < 1.0, p = 0.8$). There were no significant interactions for this parameter.

3.3. Discussion

Despite her initial difficulties in performing bimanual movements after her stroke, at the time of testing MM was able to couple bimanual movements in terms of movement onset and movement duration. Furthermore, she showed appropriate uncoupling or independence of peak velocity for incongruent bimanual movements when the targets were positioned at different distances. These results are in line with previous findings of bimanual coupling in normal subjects (Jackson et al., 1999; Kelso et al., 1979). However, MM is quite different from patient DB, a patient with contralesional sensory impairment as a result of a right anterior parietal lesion who tended to couple peak velocity inappropriately for incongruent bimanual movements (Jackson et al., 2000). Jackson et al. (2000) argue that proprioceptive cues were not available for DB's left hand, and that the inappropriate movement coupling reflects dominance for the ipsilesional limb under those conditions. In contrast to DB, MM was able to perform incongruent bimanual movements (in terms of distance) relatively normally.

4. Experiment 2

Here, we investigated MM's ability to show inter-limb independence for grasp scaling by manipulating object size.

4.1. Method

MM was asked to make unimanual or bimanual movements in much the same way as in Experiment 1. MM had to reach unimanually or bimanually towards small (3 cm diame-

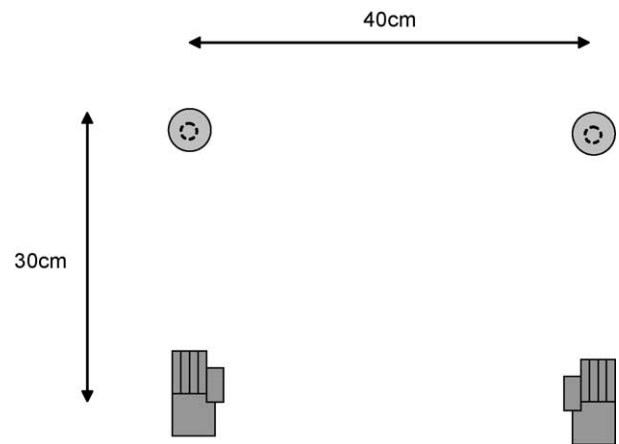


Fig. 6. Set-up for Experiment 2. MM made unimanual reaches to either small or large targets, bimanual congruent reaches (small/small; large/large) or bimanual incongruent reaches (small/large; large/small).

ter) or large targets (6 cm diameter) (see Fig. 6). The distance of the targets was fixed at 30 cm from the hand starting position and MM again completed 10 repetitions for each of the eight conditions (left small, left large, right small, right large, bimanual congruent small, bimanual congruent large, bimanual incongruent left small right large, bimanual incongruent left large right small). The conditions were randomised over trials.

4.2. Results

Again, the individual parameter values calculated in all the analyses were treated as individual subjects. Table 2 shows the mean kinematic parameters for each hand in all conditions. An independent subjects $2 \times 2 \times 3$ ANOVA was conducted containing the following factors: hand (left, right); size (small, large) and condition (unimanual, bimanual congruent, bimanual incongruent).

4.2.1. Kinematics for the transport phase

4.2.1.1. Movement duration. Movement duration did not differ significantly for hand (left = 1089 ms, right = 1028 ms; $F(1, 98) = 1.9, p = 0.2$) or for size (small = 1073 ms, large = 1048 ms; $F(1, 98) < 1.0, p = 0.4$). There was a significant effect of condition ($F(2, 98) = 36.2, p < 0.0001$). Contrasts showed that the unimanual movement durations (804 ms) were significantly shorter than both bimanual conditions (congruent = 1184 ms, $F(1, 98) = 51.6, p < 0.0001$; incongruent = 1198 ms, $F(1, 98) = 56.3, p < 0.0001$) but the two bimanual conditions had comparable movement durations ($F(1, 98) < 1.0, p = 0.8$). None of the interactions reached significance.

4.2.1.2. Peak velocity. Across the experiment, peak velocity of the right hand was higher than that for the left hand (left = 604 mm/s, right = 690 mm/s; $F(1, 101) = 17.6, p < 0.0001$). There was also a significant main effect

Table 2
Mean kinematic values for Experiment 2

	Unimanual				Bimanual—congruent				Bimanual—incongruent			
	Small		Large		Small		Large		Small		Large	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Duration (ms)	879	691	894	729	1297	1220	1143	1086	1268	1143	1076	1326
Peak velocity (mm/s)	658	828	659	874	568	589	596	624	606	591	536	639
Time to peak velocity (ms)	322	223	317	247	319	330	327	321	350	345	346	386
Deceleration time (ms)	557	468	577	481	972	888	816	812	979	794	730	921
Peak grip aperture (mm)	113	107	138	122	126	106	138	128	133	109	132	124
Time to peak grip aperture (ms)	468	353	414	516	585	644	652	733	573	721	663	695

of condition ($F(2, 101) = 26.9, p < 0.0001$). Contrasts revealed that unimanual movements had a significantly higher peak velocity than each of the two bimanual conditions (congruent, $F(1, 101) = 40.1, p < 0.0001$; incongruent, $F(1, 101) = 40.4, p < 0.0001$) but there was no difference between the two bimanual conditions ($F(1, 101) < 1.0, p = 0.9$). There was a significant interaction of Hand \times Condition ($F(1, 101) = 6.5, p < 0.005$). The right hand had a significantly higher peak velocity than the left hand, but only in the unimanual condition (left = 660 mm/s, right = 848 mm/s; $F(1, 34) = 35.4, p < 0.0001$). Peak velocity was comparable across the hands for the two bimanual conditions (congruent, left = 582 mm/s, right = 606 mm/s, $F(1, 34) < 1.0, p = 0.4$; incongruent, left = 569 mm/s, right = 615 mm/s, $F(1, 33) < 1.0, p = 0.4$). There were no other significant main effects or interactions.

4.2.1.3. Time to peak velocity. TTPV was equivalent for the left and right hands (left = 330 ms, right = 305 ms; $F(1, 96) = 1.3, p = 0.3$) and also for small and large targets (small = 313 ms, right = 325 ms; $F(1, 96) < 1.0, p = 0.6$). There was a significant main effect of condition ($F(2, 96) = 5.7, p < 0.005$). Contrasts showed TTPV to be shorter for unimanual movements (280 ms) than for movements in the bimanual congruent condition (324 ms; $F(1, 96) = 4.2, p < 0.05$) and in the bimanual incongruent condition (355 ms; $F(1, 96) = 10.9, p < 0.005$); however, the two bimanual conditions were comparable ($F(1, 96) = 1.8, p = 0.2$). No other main effects or interactions proved significant.

4.2.1.4. Deceleration time. The left and right hands did not differ in the time taken between TTPV and movement end (left = 768 ms, right = 729 ms, $F(1, 99) < 1.0, p = 0.3$), nor did deceleration times for small and large targets (small = 769 ms, large = 731 ms, $F(1, 99) = 1.3, p = 0.3$). There was a significant main effect of condition ($F(2, 99) = 24.1, p < 0.0001$). Contrasts showed that deceleration time for the unimanual condition (524 ms) was significantly shorter than for the bimanual congruent condition (870 ms, $F(1, 99) = 37.9, p < 0.0001$) and the bimanual incongruent condition (856 ms, $F(1, 99) = 34.5, p < 0.0001$). However, the two bimanual conditions were equivalent ($F(1, 99) < 1.0, p = 0.8$). There were no other significant main effects or interactions.

4.2.1.5. Temporal coupling of the transport phase. Temporal coupling was analysed in the same way as it was in Experiment 1. For Experiment 2, mean movement onset lag was -25 ms suggesting close coupling between the limbs. Movement onset lag did not differ significantly between the two bimanual conditions (means: congruent = -19 (13) ms; incongruent = -32 (14) ms; $F(1, 33) < 1.0, p = 0.5$). In addition, a significant correlation was found between the left and right hands for movement onset ($r = 0.9, p < 0.0001$).

The mean movement endpoint lag was -11 ms showing close coupling between the limbs. Lags did not vary significantly between conditions (means: congruent = 43 (48) ms; incongruent = -66 (47) ms; $F(1, 37) = 2.6, p = 0.1$) and were significantly correlated ($r = 0.7, p < 0.0001$).

In summary, for the transport phase in Experiment 2, MM showed appropriate coupling of the limbs with bimanual movements demonstrating the typical 'costs' associated with bimanual movements compared with unimanual movements.

4.2.2. Kinematics for the grasp phase

4.2.2.1. Peak grip aperture. The ANOVA revealed a significant main effect of hand ($F(1, 106) = 89.6, p < 0.0001$) with the left hand shaping larger than the right (left = 130 mm, right = 116 mm). Grip apertures to large targets were significantly greater than to small targets (small = 116 mm, large = 130 mm, $F(1, 106) = 93.5, p < 0.0001$). There was also a significant main effect of condition ($F(2, 106) = 3.9, p < 0.05$). Contrasts revealed that peak grip aperture was narrower for the unimanual condition (119 mm) than the bimanual congruent condition (125 mm, $F(1, 106) = 6.1, p < 0.05$) and the bimanual incongruent condition (124 mm, $F(1, 106) = 5.5, p < 0.05$). However, the two bimanual conditions were equivalent ($F(1, 106) < 1.0, p = 0.9$). In addition, there was a significant two-way interaction of Size \times Condition ($F(2, 106) = 7.3, p < 0.005$), and a significant three-way interaction for Hand \times Size \times Condition ($F(2, 106) = 6.8, p < 0.005$). The difference in behaviour between the hands becomes clear when the interactions are explored fully. For the right hand, while there is a significant difference in scaling to different sized objects ($F(1, 53) = 83.5, p < 0.0001$), this scaling is consistent across conditions ($F(2, 53) < 1.0, p = 0.5$) and there was no significant Size \times Condition interaction ($F(2, 53) = 1.3, p = 0.3$).

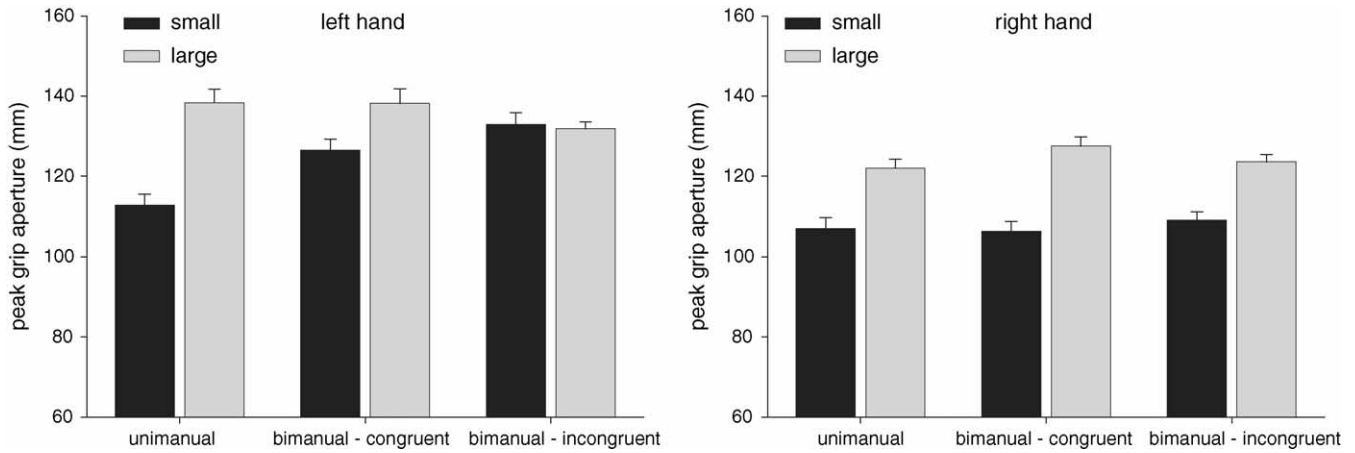


Fig. 7. PGA values (and error bars) for the left and right hands. While the right hand remains relatively stable across conditions, the left (contralesional) hand shows a dependency on the right (ipsilesional) target.

However, for the left hand, while again there was a significant main effect of size ($F(1, 53) = 26.1, p < 0.0001$), this scaling changed as a function of condition ($F(2, 53) = 3.6, p < 0.05$) and there was a significant Size \times Condition interaction ($F(2, 53) = 10.6, p < 0.0005$). If the Size \times Condition interaction for each hand is explored further, it can be seen that the right hand demonstrates significantly different scaling to small and large objects for each condition (unimanual, small = 106.9 mm, large = 122.0 mm, $F(1, 19) = 18.2, p < 0.005$; bimanual congruent, small = 106.3 mm, large = 127.5 mm, $F(1, 18) = 39.9, p < 0.0001$; bimanual incongruent, small = 109.0 mm, large = 123.6 mm, $F(1, 18) = 28.6, p < 0.0001$). The left hand also showed a significant size effect for unimanual (small = 112.8 mm, large = 138.4 mm, $F(1, 17) = 35.2, p < 0.0001$) and bimanual

congruent movements (small = 126.5 mm, large = 138.2 mm, $F(1, 18) = 6.6, p < 0.025$) but this was lost for bimanual incongruent movements (small = 133.0 mm, large = 131.9 mm, $F(1, 18) < 1.0, p = 0.7$) (see Fig. 7). Grip profiles from representative trials of the bimanual incongruent condition are shown in Fig. 8.

4.2.2.2. *Time to peak grip aperture.* The time from movement onset to when peak grip aperture was reached was equivalent for each hand (left = 0.56 s, right = 0.61 s, $F(1, 99) = 2.1, p = 0.2$) and for the two sizes of target (small = 0.55 s, large = 0.62 s, $F(1, 99) = 2.4, p = 0.1$). There was a significant main effect of condition ($F(2, 99) = 16.7, p < 0.0001$). Contrasts revealed that MM was significantly faster to reach peak grip aperture in the unimanual condition (0.43 s)

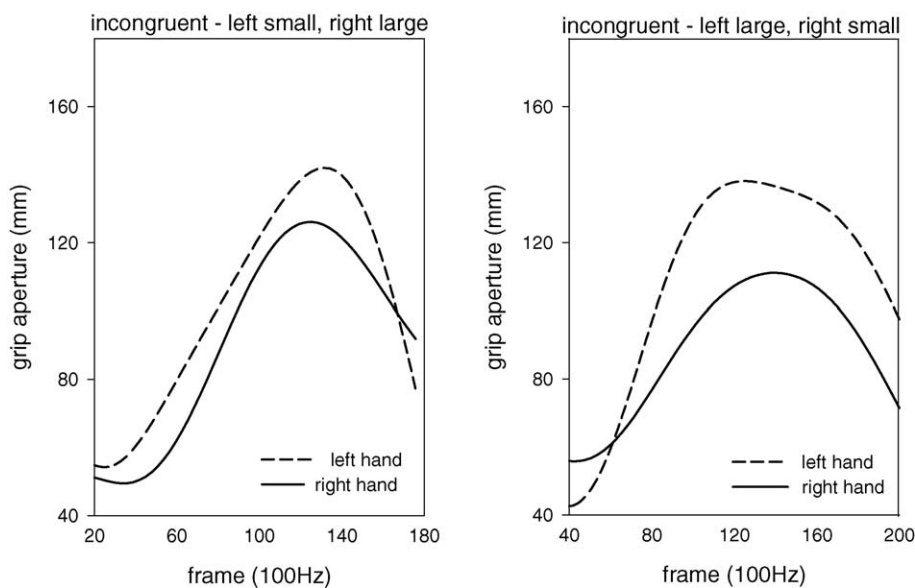


Fig. 8. Representative grip aperture for the left and right hands for the incongruent conditions in Experiment 2. While the right hand scales normally, the left hand shows an abnormal dependence related to the target grasped by the right hand.

than in both the bimanual congruent condition (0.65 s, $F(1, 99)=24.1$, $p<0.0001$) and the bimanual incongruent condition (0.66 s, $F(1, 99)=26.2$, $p<0.0001$). However, the two bimanual conditions were equivalent ($F(1, 99)<1.0$, $p=0.8$). None of the interactions approached significance.

In summary, MM showed appropriate scaling for unimanual movements to the small and large object, with both the left and right hands, though the left hand scaled wider. There was also appropriate scaling of grasp in the bimanual congruent condition. However, the interaction between the hands broke down in the bimanual incongruent condition. The left hand was modulated by the grip aperture adopted for the right hand while the right hand grip aperture showed no effect of the left hand.

4.3. Discussion

In Experiment 2 as in Experiment 1, MM showed relatively normal coupling for the transport phase of bimanual movements. However, here we were primarily interested in whether MM was able to scale the contralesional hand appropriately to the size of the target. In this respect, the experiment revealed a number of interesting findings. Firstly, and most noticeably, the contralesional hand did not demonstrate the same pattern of performance as the ipsilesional hand across conditions. It is tempting to explain the results in terms of a contralesional deficit alone. However, closer inspection shows that the relative scaling of each hand is more illuminating. On trials involving incongruent bimanual movements, the contralesional left hand demonstrated an influence of the ipsilesional hand; relative to the unimanual baseline, the grip aperture was smaller for large objects and larger for small objects. In contrast, there was no modulation of grasp aperture for the ipsilesional hand. This represents a significant shift away from the behaviour seen in normal subjects where both hands share the cost of bimanual activity (Castiello et al., 1993; Dohle et al., 2000; Jackson et al., 1999). The bimanual actions of MM here are indicative of an attentional bias in favour of the ipsilesional target and/or the ipsilesional hand; although the contralesional hand acts appropriately under unimanual movement conditions, grasp programming is unduly influenced by the ipsilesional action being conducted concurrently. This may be similar to the inappropriate coupling of the transport component of prehension reported for patient DB by Jackson et al. (2000). In DB's case, the transport component of movement made by the contralesional limb was coupled to that made by the ipsilesional limb even when the reached-for objects were at different distances. In MM's case, there was a complete lack of an effect of the grip aperture of the contralesional hand on the ipsilesional hand, while the ipsilesional hand strongly influenced the contralesional one. This suggests a classic 'winner takes all' situation where the ipsilesional hand wins the selection of the parameters for the grasp action

5. General discussion

We investigated bimanual coordination in a patient, MM, who had motor neglect and extinction following stroke. MM demonstrated an interesting pattern of performance when required to make bimanual reach-to-grasp movements to objects. When the objects were at different distances, MM showed appropriate uncoupling of the 'reach' components of her actions. For example, there was a cross-over of peak velocities with the contralesional (left) hand showing higher peak velocity than the ipsilesional (right) hand when the left object was far and the right near; the opposite occurred when the distances of the objects reversed. There was also some 'cost' to this, since peak velocities for both hands were lower for bimanual than for unimanual movements. In contrast, a different pattern arose when the objects were at the same distance but were different sizes. The grasp components of the actions were not uncoupled and there was dominance of the ipsi-(right) over the contralesional (left) hand. The ipsilesional hand was scaled appropriately to the size of the object, but this did not change as a function of whether the other object was the same or a different size. However, the contralesional hand was not scaled appropriately. Grip aperture to a small object was wider than in the unimanual and congruent bimanual condition; grip aperture to a large object was smaller than in the unimanual and congruent bimanual conditions.

Since the impairment in the grasp component emerged in bimanual but not unimanual conditions, it may be considered as part of the syndrome of motor extinction. Motor extinction has only a limited history of study but has been shown to adversely affect contralesional movement initiation (hypokinesia) (Valenstein & Heilman, 1981) and the sustaining of movement (Mattingley, 2002). It is conceivable that, if an attentional bias in movement can lead to contralesional hypokinesia and hypometria, then other aspects of motor production might be similarly affected. The present data suggest that aspects of grasp production can be affected, while the reach components of an action are relatively spared. The deficit in the grasp component indicates a bias in motor programming, with greater weight applied to this component of the ipsi-compared with the contralesional motor programme, when both are effected simultaneously. The problem was greater for the grasp than the reach component of MM's actions, perhaps representing a selective deficit in the grasp component. This would fit with Jeannerod's (1981) original distinction between reaching and grasping actions.

The selective effect of the deficit on the grasp component of actions fits with a 'motor competition' account and it presents some difficulties to some other accounts, suggesting that performance is affected by a more general attentional bias. For example, one alternative account is that the deficit is induced by a bias in visual attention to the object on the ipsilesional side. Such an attentional bias could arise if motor programmes feedback to influence visual attention (cf. Deubel & Schneider, 2004; Humphreys et al., 2004), and

there is stronger activation of a motor response with the ipsilesional limb. Due to this stronger motor activation, MM might orient to the ipsilesional side, and the object on that side then dominates selection of the appropriate grip. In simple terms, however, this account would also predict an affect on the transport component of the action, which was not supported here. The pattern of this deficit on the grasp component specifically under bimanual movement conditions, provides a form of double dissociation when considered in conjunction with the data from DB (Jackson et al., 2000). DB also showed a deficit in bimanual action, but this affected the transport component of reaching. However, Jackson et al. did not test DB on bimanual movements to incongruently sized objects as in Experiment 2 here. It is, therefore hard to tell if contralateral grip was abnormally affected by the ipsilesional side. It could be that both were affected in this case. MM shows a selective grip affect but this may reflect the more difficult component, holding a higher position in the hierarchy of motor programming. Nevertheless the attentional account can be maintained if we distinguish between the affects of attention on the grasp and transport components of movement. For example, if attention influences the relatively late stages of action, then it might exert a greater effect on grip aperture as this may be programmed later in the reach and grasp action (Jeannerod, 1981).

Whichever account of MM's performance is favoured, the data demonstrate that there can be differential effects of a brain lesion on bimanual motor coupling. The coupling may be relatively intact for reach components of action, but not for the grasp component. The data emphasise the distinction between these two components of motor programming.

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References

- Bootsma, R. J., Marteniuk, R. G., MacKenzie, C. L., & Zaal, F. T. (1994). The speed-accuracy trade-off in manual prehension: Effects of movement amplitude, object size and object width on kinematic characteristics. *Experiments Brain Research*, *98*, 535–541.
- Castiello, U., Bennett, K. M. B., & Stelmach, G. E. (1993). The bilateral reach to grasp movement. *Behavioural Brain Research*, *56*, 43–57.
- Chieffi, S., Gentilucci, M., Allport, A., Sasso, E., & Rizzolatti, G. (1993). Study of selective reaching and grasping in a patient with unilateral parietal lesion. Dissociated effects of residual spatial neglect. *Brain*, *116*(Pt 5), 1119–1137.
- Deubel, H., & Schneider, W. X. (2004). Attentional selection in sequential manual movements, movements around an obstacle and in grasping. In G. W. Humphreys & M. J. Riddoch (Eds.), *Attention in action*. Hove: Psychology Press.
- Dohle, C., Ostermann, G., Heftner, H., & Freund, H. J. (2000). Different coupling for the reach and grasp components in bimanual prehension movements. *Neuroreport*, *11*, 3787–3791.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, *79*, 39–88.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal Experimental Psychology*, *47*, 381–391.
- Gado, M., Hanaway, J., & Frank, R. (1979). Functional anatomy of the cerebral cortex by computed tomography. *Journal of Computer Assisted Tomography*, *3*, 1–19.
- Humphreys, G. W., Riddoch, M. J., Punt, T. D., Linnell, K. J., Edwards, M. G., & Wing, A. M. (2004). Attending to what you are doing: Neuropsychological and experimental evidence for interactions between perception and action. In G. W. Humphreys & M. J. Riddoch (Eds.), *Attention in action*. Hove: Psychology Press.
- Jackson, G. M., German, K., & Peacock, K. (2002). Functional coupling between the limbs during bimanual reach-to-grasp movements. *Human Movement Science*, *21*, 317–333.
- Jackson, G. M., Jackson, S. R., Husain, M., Harvey, M., Kramer, T., & Dow, L. (2000). The coordination of bimanual prehension movements in a centrally deafferented patient. *Brain*, *123*(Pt 2), 380–393.
- Jackson, G. M., Jackson, S. R., & Kritikos, A. (1999). Attention for action: Coordinating bimanual reach-to-grasp movements. *British Journal of Psychology*, *90*(Pt 2), 247–270.
- Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long & A. Baddeley (Eds.), *Attention and performance IX* (pp. 153–169). Hillsdale: Lawrence Erlbaum Associates.
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, *32*, 369–380.
- Kelso, J. A., Putnam, C. A., & Goodman, D. (1983). On the space-time structure of human interlimb co-ordination. *The Quarterly Journal of Experimental Psychology A*, *35*(Pt 2), 347–375.
- Kelso, J. A., Southard, D. L., & Goodman, D. (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 229–238.
- Mattingley, J. B. (2002). Spatial extinction and its relation to mechanisms of normal attention. In H. O. Karnath, A. D. Milner, & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 289–309). Oxford: Oxford University Press.
- Mattingley, J. B., & Driver, J. (1997). Distinguishing motor and sensory deficits after parietal damage: An evaluation of response selection biases in unilateral neglect. In P. Thier & H.-O. Karnath (Eds.), *Parietal lobe contributions to orientation in 3D space* (pp. 309–337). Berlin: Springer-Verlag.
- Meador, K. J., Watson, R. T., Bowers, D., & Heilman, K. M. (1986). Hypometria with hemispatial and limb motor neglect. *Brain*, *109*, 293–305.
- Monno, A., Temprado, J. J., Zanone, P. G., & Laurent, M. (2002). The interplay of attention and bimanual coordination dynamics. *Acta Psychologica (Amsterdam)*, *110*, 187–211.
- Posner, M. I., Inhoff, A. W., & Friedrich, F. J. (1987). Isolating attentional systems—A cognitive-anatomical analysis. *Psychobiology*, *15*, 107–121.
- Robertson, I. H., McMillan, T. M., MacLeod, E., Edgeworth, J., & Brock, D. (2002). Rehabilitation by limb activation training reduces left-sided motor impairment in unilateral neglect patients: A single-blind randomised control trial. *Neuropsychological Rehabilitation*, *12*, 439–454.
- Serrien, D. J., Nirkko, A. C., Lovblad, K. O., & Wiesendanger, M. (2001). Damage to the parietal lobe impairs bimanual coordination. *Neuroreport*, *12*, 2721–2724.
- Swinnen, S. P., Jardin, K., & Meulenbroek, R. (1996). Between-limb asynchronies during bimanual coordination: Effects of manual dominance and attentional cueing. *Neuropsychologia*, *34*, 1203–1213.

- Valenstein, E., & Heilman, K. M. (1981). Unilateral hypokinesia and motor extinction. *Neurology*, *31*, 445–448.
- Vallar, G., Bottini, G., & Sterzi, R. (2003). Anosognosia for left-sided motor and sensory deficits, motor neglect, and sensory hemi-inattention: Is there a relationship? *Progress in Brain Research*, *142*, 289–301.
- Wilson, B., Cockburn, J., & Halligan, P. (1987). Development of a behavioral test of visuospatial neglect. *Archives of Physical Medicine Rehabilitation*, *68*, 98–102.
- Wuyts, I. J., Summers, J. J., Carson, R. G., Byblow, W. D., & Semjen, A. (1996). Attention as a mediating variable in the dynamics of bimanual coordination. *Human Movement Science*, *15*, 877–897.