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Bimanual reaching across the hemispace: Which hand is yoked to which?

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ABSTRACT

When both hands perform concurrent goal-directed reaches, they become yoked to one another. To investigate the direction of this coupling (i.e., which hand is yoked to which), the temporal dynamics of bimanual reaches were compared with equivalent-amplitude unimanual reaches. These reaches were to target pairs located on either the left or right sides of space; meaning that in the bimanual condition, one hand's contralateral (more difficult) reach accompanied by the other hand's ipsilateral (easier) reach. By comparing which hand's difficult reach was improved more by the presence of the other hand's easier ipsilateral reach, we were able to demonstrate asymmetries in the coupling. When the cost of bimanual reaching was controlled for the contralateral reaching left hand's performance was improved, suggesting that the left hand is yoked to the right during motor output. In contrast, the right hand showed the greatest improvements for contralateral reaching in terms of reaction time, pointing toward a dominant role for the left hand in the processes prior to movement onset. The results may point toward a mechanism for integrating the unitary system of attention with bimanual coordination.

1. Introduction

Bimanual coordination is a relatively common feature of goal-directed interaction outside of the laboratory in humans. Both hands tend to play complementary, yet distinct, roles in many daily activities, such as tying shoelaces, buttoning shirts, and even writing on a sheet of paper. Despite the apparent independence of the hands in these tasks, many experimental studies have indicated that there are severe temporal constraints upon the hands during discrete and rhythmic bimanual coordination (Corcos, 1984; Kelso, 1984; Kelso, Putnam, & Goodman, 1983; Kelso, Southard, & Goodman, 1979; Marteniuk, Mackenzie, & Baba, 1984, Swinnen, 2002). Here, we investigate how this dichotomy is resolved within the motor system by determining if one hand is yoked to the other during simple visually-guided bimanual reaches.

When individuals move both hands together, they tend to temporally synchronise the movement of one hand with the other. This synchronisation effect is even strong enough to induce unintentional shifts from anti-phase coordination (i.e., moving out of time) to in-phase coordination (moving in time – Kelso, 1984; see Swinnen (2002) for review). Recent work by De Poel, Peper, and Beek (2007) indicates that this temporal synchronisation is not symmetrical. Rather than synchronising to a 'middle ground' (the equivalent of both limbs making simultaneous phase shifts of 90°), the non-dominant limb was more strongly influenced by the dominant limb than vice versa (see also Byblow, Carson, & Goodman, 1994; De Poel, Peper, & Beek, 2006). Interestingly, this asymmetry appears to be modulated by the direction of attention during the task itself (De Poel, Peper, & Beek, 2008), mirroring suggestions from earlier research that attention may be laterally-focussed during bimanual coordination as an expression of cerebral lateralization (Peters, 1981).

Similar effects of temporal synchronisation have been demonstrated during discrete bimanual tasks. When reaching with both hands, the usual pattern of temporal asymmetries evident in one-handed reaches with either limb (the small left hand reaction time advantage and the larger right hand movement duration advantage) are ameliorated, and the hands start and finish their reaches at the same time (Kelso et al., 1979). This temporal coupling even takes place when the hands must make movements of different amplitudes from one another – with bimanual reaches taking substantially longer to terminate than unaccompanied movements of equivalent amplitude (Kelso et al., 1983). Functionally, this means that the hand with the shorter reach is slowed down by the hand with the more difficult, longer reach. It is clear that, at least conceptually, the timing mechanisms of both rhythmic and discrete bimanual coordination are similar. However, despite valiant efforts to computationally model discrete movements as truncated rhythmic movements (e.g., Ronsse, Sternad, & Lefèvre, 2009), the differences in the locus of neural activation between these coordination modes (Schall, Sternad, Osu, & Kawato, 2004) suggests that such a generalization may be inadequate.

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With the current study, we aimed to determine whether evidence for a leading role for the dominant hand could be demonstrated during a discrete bimanual reaching task. In contrast to the work examining asymmetries during rhythmic bimanual movements, only very limited evidence exists of either hand 'giving more ground' than the other during discrete bimanual tasks. Marteniuk et al. (1984) elicited small asymmetries in the direction of the coupling, by comparing bimanual reaches with equivalent unimanual reaches while 'handicapping' one hand with a heavier stylus than the other. As the handicapped right hand slowed the left hand more than the converse condition, it could be suggested that the left hand was 'bound' to the right hand. However Martenuik's study failed to provide compelling evidence of asymmetrical yoking in all the subjects, perhaps due to variability of many unimanual performance measures. An obvious way to improve the chances of demonstrating asymmetries in coupling would be to further increase the magnitude of the baseline (i.e., unimanual) asymmetries – increasing the difference between uncoupled unimanual hand differences with those in a coupled bimanual reach. Hemispatial asymmetries may allow just such a reduction in the performance of one hand relative to the other.

When a hand performs a reach into its own space, the movement is completed in a shorter duration and higher peak velocities than an equivalent amplitude reach across the body midline. The mechanisms underlying this ipsilateral/contralateral reaching asymmetry are still under some debate. Some researchers have suggests that the contralateral reaching deficits are merely an expression of the increased attentional demands of common stimulus–response compatibility effects (see Procter and Reeve (1990) for review). However, most researchers tend to view the hemispace asymmetry in terms of inter- vs. intra-hemisphere processing. Therefore, for an ipsilateral reach, the hemisphere that processes the visual target is also responsible for the eventual motoric output. Therefore the transfer from one hemisphere to the other that must occur prior to a contralateral reach somehow slows the overall performance (Velay & Benoit-Dubrocard, 1999). Conversely, studies by Carey, Hargreaves, and Goodale (1996) and Carey and Otto-de Haart (2001) have found compelling evidence that the within/between hemisphere processing theory cannot fully account for the deficits seen when reaching across the body midline. Carey and colleagues instead proposed that the difficulty in reaching across the body midline was due mostly to biomechanical factors, such as the larger centre of mass around the two-joint system necessary for contralateral reaching (ipsilateral reaching generally requires little more than extension of the elbow joint). It must be noted however that for the purposes of the current experiments, the underlying causes of the hemispatial reaching asymmetries are not relevant. The crucial point here is that movements made into the contralateral hemispace are slowed relative to ipsilateral equivalents. Thus, in order for bimanual reaches to left or right space to be synchronised in time, one hand must be slowed down or sped up, relative to the performance that can be attained when reaching in a unimanual circumstance.

With the current study, we aimed to determine which hand was yoked to which by combining the contralateral reaching disadvantage (Carey et al., 1996) with the temporal yoking usually seen between the hands during bimanual reaches of different amplitudes (Kelso et al., 1983). Participants reached with both hands at the same time toward target pairs that were different amplitudes away from the start location in the right or left hemispace. Therefore, one hand performed an easy, ipsilateral reach while its counterpart performed a more difficult, contralateral reach to contact the targets – imposing a kinematic (and perhaps more naturalistic) deficit upon one hand, analogous to the differentially weighted styli described by Marteniuk et al. (1984). This paradigm contrasts the majority of bimanual reaching tasks, where both hands tend to reach only into their respective ipsilateral sides of space (e.g., Kelso et al., 1979; Marteniuk et al., 1984; however, see Experiment 3 from Kelso et al. (1983) for an exception).

To determine which hand was yoked to which, the changes in performance between bimanual and equivalent unimanual reaches to either hemispace were examined. It was hoped that this task would give an indication of which hand's performance was more malleable to the temporal coupling exhibited during bimanual reaching. One possibility would be that both hands tend toward a central 'compromise' during bimanual reaching, indicating that the coupling was symmetrical, as implied by the work of Kelso and colleagues (1979), Kelso and colleagues (1983). Alternatively, the right hand's performance may be more affected by the left hand, presumably by reducing its level of performance to accommodate the, comparatively less able, non-dominant limb. However, based on the rhythmic bimanual studies of Peters (1981) and De Poel et al. (2006), De Poel et al. (2008), we predicted that the right hand would be 'in-charge' of the left. This behavioural profile would lead to increased changes in the left hand's performance between unimanual and bimanual reaching to equivalent targets. These alterations may even take the form of an ipsilateral reaching right hand using the yoking to improve the performance of a contralateral reaching left hand, relative to an equivalent unimanual reach.

Unfortunately, such a direct comparison may not be feasible. A large body of evidence has demonstrated that bimanual reaching incurs a substantial cost in terms of reaction time and movement duration compared to unimanual equivalents (see Ohtsuki (1994) for review). The cause of this bimanual cost is not only largely undefined, but also refractory to the purpose of the current work. We therefore decided to partial out this bimanual cost from the inferential analyses where bimanual and unimanual reaches are compared, in order to get a clearer picture of any interactions between hand, space and coupling. To normalise the unimanual reaching scores to those of the bimanual conditions in all measures, the overall unimanual mean for a particular measure was subtracted from the overall bimanual mean. The value yielded from this calculation – the 'bimanual cost' (reported for each measure in the results section) was then added to, or subtracted from, the unimanual scores as appropriate. This adjustment to the unimanual values for any particular measure served to make comparisons between bimanual and unimanual reaching more readily interpretable.

2. Methods

2.1. Participants

Eighteen postgraduate students and staff members of the University of Aberdeen School of Psychology (eight male) took part in this study (mean age = 27.5 years, $SD = 6.4$). All participants were right-handed (mean score = 26.4/30, $SD = 4.9$, as measured by a modified version of the Waterloo Handedness Questionnaire; Steenhuis & Bryden, 1989), with 13 of the sample showing right eye sighting dominance. Participants were naïve to the hypothesis and gave written informed consent prior to testing. All procedures were approved by the Ethics Committee of the School of Psychology at the University of Aberdeen.

2.2. Apparatus and data reduction

A horizontal light emitting diode (LED) grid and custom PC software were used to deliver the central fixation and target stimulus. Infrared reflective markers were attached to the participant's index fingers. The position of these markers were monitored with a three-camera ProReflex motion analysis system (Qualisys Inc.), recording at 240 Hz. The camera positions were calibrated prior